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VOLUME XL

(1954 Meeting)

PART I. BOTANY AND FORESTRY

1955

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GRACE E. POTTER AND WILLIAM R. STEINHOFF

PART I. BOTANY AND FORESTRY

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PART I. BOTANY AND FORESTRY

BOTANY

Papers of the Michigan Academy of Science, Arts, and Letters,
Vol. XL, 1955 (1954 Meeting)

A NEW SPECIES OF CAMPTOMERIS, AND FURTHER NOTES ON THE GENUS

ERNST A. BESSEY

THROUGH the kindness of Professor Hazime Yoshii, Professor of Plant Pathology, Kyushu University, Fukuoka, Japan, I received specimens of *Astragalus sinicus* L. that were affected with a fungus which he suggested might belong "not far from *Camptomeris*." After I had confirmed the correctness of this suggestion, he generously permitted me to study and describe this new fungus.

Camptomeris astragali, sp. nov.

(Pl. I, Figs. 1–5)

Megalophyses late piriformes, 32–64 μ alt. $\times$ 29–67 μ diam. in parte suprastomatale, pallide brunneae, rarius atrobrunneae. Conidiophora atrobrunnea, 300–1,500 in superiore dimidio singularum megalophysum, nonseptata, lateralia aliquanto applanata, 10–14 $\times$ 4–8 μ, superiora 16.8–22.4 $\times$ 5–8.4 μ. Conidia singulatim orta ad apices conidiophororum, pallide brunnea, non nunquam atrobrunnea, globosa sive piriformia, saepe paululo angustata ad basim, paulo minute verruculosa in dimidio apicale, 12–21 $\times$ 10–14 μ, rarissime uniseptata, 22–32 $\times$ 7.4–13.8 μ. Sporodochidia 54–93 $\times$ 45–86 μ, singulatim vel densiuscule conferta.

Hab. hypophylle in foliis *Astragali sinici* L., Kagoshima, Kyushu, Japonia. Legit Prof. Hazime Yoshii, 1950 et 1952 (specimen typicum). Specimen typicum in Herb. Michigan State College conservatum.

The megalophyses are broadly pyriform (Pl. I, Figs. 3–4), the top often rather flattened, generally upright but sometimes decumbent, especially in the cases (8 to 9 per cent) in which two (very rarely three) emerge from one stoma. The stomata are ruptured by the emergence of the megalophyses, whose basal diameter is considerably greater than the diameter of the stomatal opening. The megalophyses are 32–64 μ tall and 29–67 μ broad in the enlarged

upper portion. The lower portion of the fully grown megalophysis, above the level of the host epidermis, is free from conidiophores (Pl. I, Fig. 3). On the immature megalophyses the conidiophores begin to form at the center of the top, and this development progresses outward and downward until the upper third or half is covered by the mass of densely packed conidiophores. At the emergent base of the megalophysis a few stout, brown, rootlike hyphae are visible, arising from the subepidermal hypostroma, which is made up of numerous polyhedral, light-brown cells.

The nonseptate conidiophores are closely packed and, depending upon the size of the megalophysis, may vary from a few hundred up to well over 1,500 (Pl. I, Figs. 2–4). Most of those arising from the top are nearly straight and isodiametric. They are slightly narrowed at the base to the point of attachment. The more laterally placed conidiophores are somewhat flattened, and they tend to curve upward a little, even becoming slightly spoon-shaped (Pl. I, Fig. 5 *e–g*). Each conidiophore bears terminally a single conidium (Pl. I, Fig. 5 *f–g*). In color the conidiophores are often darker than the wall of the megalophysis, although sometimes this also is dark brown. When the conidiophores fall away they leave alveolate markings on the surface of the megalophysis. The lateral conidiophores are 10–14 × 4–8 μ, and those attached at or near the top measure 16.8–22.4 × 5–8.4 μ.

The conidia are globoid or broadly obpyriform, often quite irregular, sometimes a little narrowed toward the base and slightly papillate at the apex. They are pale fuscous, a little lighter in color than the conidiophores. Each shows a basal scar. They are minutely verruculose over the upper portion and smooth on the lower half. The roughening consists of fine lines of minute verrucosities about 1.0–1.2 μ apart. These lines converge toward the apex of the spore, but diverge toward its middle. In rare cases (less than one in two hundred), the spore is transversely septate and the lower cell is entirely smooth, while the narrower upper cell is somewhat roughened. The unicellular conidia (Pl. I, Fig. 5 *a–b*) are 12–21 × 10–14 μ, and the rare 2-celled spores (Pl. I, Fig. 5 *c–d*) are 22–32 × 7.4–13.8 μ.

The emerging megalophysis with its attached conidiophores and conidia has been named (Bessey, 1953) a sporodochidium. These sporodochidia may be free from one another, or they may be clustered into sorus-like groups, 0.2–2.0 mm. in diameter (Pl. I, Fig. 1). They are dark fuscous, and vary from 54–93 × 45–86 μ. They

occur hypophyllously on the leaflets of *Astragalus sinicus* L. and do not cause noticeably discolored spots so far as could be determined from the dried leaves, which were all that were available for study. On preliminary examination, even with a pocket lens, I took these clusters of sporodochidia to be the sori of some species of Uromyces, and not until they were examined under the compound microscope was their true nature revealed.

The two lots of specimens studied were collected by Professor Hazime Yoshii in rice paddies at Kagoshima, Kyushu, Japan, where the host plants are grown for green-manuring purposes. One lot was collected in June 1950, and the other, and better, lot was collected in June 1952. The second lot has been designated the type. Both lots are preserved in the Mycological Herbarium of Michigan State College.

The genus Camptomeris was described by H. Sydow in 1927 with the single species *C. calliandrae*, from Costa Rica, on living leaves of *Calliandra similis* Sprague & Riley. In this type specimen (Pl. I, Fig. 6) there are only from 6 to 19 conidiophores to each megalophysis, and these are in only one or two rows. Each is septate once, near the base. In *C. floridana* Bessey (Pl. II, Figs. 1–2), the megalophyses are larger and bear from 16 to 105 conidiophores, each usually uniseptate, in several series. In *C. martynii* Bessey (Pl. II, Figs. 3–4), the 16–38 conidiophores are nonseptate and also occur in several series. In *C. verruculosa* (Syd.) Bessey (Pl. II, Figs. 5–6), the 16–82 conidiophores are spreading, in one or two series, and rarely septate near the base. In all of these species the conidia are mostly 3- to 4-septate and are from two to four times as long as broad. In one species, *C. desmanthi* Ciferri, the conidia are regularly only 2-celled; they are oblong, and about four times as long as broad. In my tentative monograph of the genus (Bessey, 1953), I recognized eight species, while Hughes (1952), who lacked access to some of the material studied by me, recognized only five. All eight species were found on Mimosaceae, in tropical and subtropical regions. The production of more or less well-developed megalophyses (not clearly distinguishable in *C. albizziicola* (Thirumalachar & Narasimhan) Bessey) is the most noticeable common character. The conidia in all eight are from three to five times as long as broad and are always septate, mostly two to three times.

Camptomeris astragali differs in occurring on a host of the family

Fabaceae instead of Mimosaceae, in the very large number of conidiophores to a megalophysis, in the short, mostly one-celled, globoid or pyriform conidia, and in the frequent emergence of two megalophyses through the same stoma.

Recently Dr. C. V. Subramanian (1952) has described and figured from Madras, India, a fungus growing hypophyllously on the leaves of *Crataeva religiosa* (Capparidaceae); he named it "*Camptomeris crataevae* n. sp." Its spores are oblong to oblong-obclavate, 2- to 3-septate, borne singly on unbranched conidiophores which are uniseptate near the base. These burst through the epidermis from the hypostroma. No megalophyses are described or figured. Until specimens that have been requested are received and studied, I shall be uncertain whether this fungus belongs to Camptomeris. The conidia and conidiophores seem to be rather typical of the genus, but the host family is very distant from that of the rest of the known species.

I am grateful to Professor Yoshii for the privilege of examining and naming the specimen on Astragalus. My gratitude is also great toward Professor Constantine J. Alexopoulos, of Michigan State College, who very generously gave of his time and skill in making the photomicrographs used in the illustration of this paper.

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Michigan State College
East Lansing, Michigan

PLATES I–II

EXPLANATION OF PLATE I

FIGS. 1–5. *Camptomeris astragali*, sp. nov.

FIG. 1. Top view of cluster of sporodochidia. About × 100

FIG. 2. Single sporodochidium with surrounding conidia. × 500

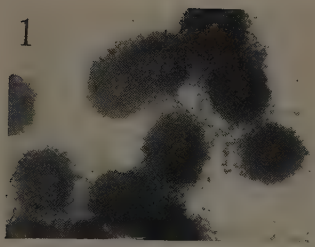
FIG. 3. Lateral view of megalophysis, with conidiophores not quite mature. About × 667

FIG. 4. Lateral view of broken megalophysis, with conidiophores bearing conidia. About × 500

FIG. 5. Conidia and conidiophores: *a–b*, lateral view of nonseptate conidia; *c–d*, lateral views of uniseptate conidia; *e*, view from above of a lateral conidiophore; *f–g*, lateral views of conidiophores bearing immature conidia. About × 667

FIG. 6. *Camptomeris calliandrae* Sydow

FIG. 6. Top view of three sporodochidia from specimen collected by Sydow in the type locality. About × 220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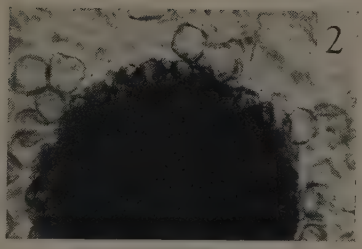
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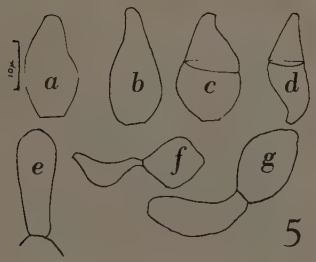
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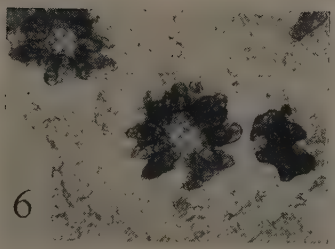
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EXPLANATION OF PLATE II

FIGS. 1–2. *Camptomeris floridana* Bessey

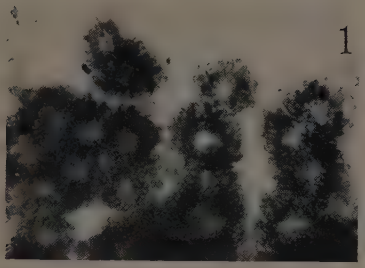
FIG. 1. Top view of cluster of sporodochidia. About × 100
FIG. 2. Conidia much enlarged. About × 400

FIGS. 3–4. *Camptomeris martynii* Bessey

FIG. 3. Top view of cluster of sporodochidia. About × 100
FIG. 4. Sporodochidia and spores enlarged further. About × 150

FIGS. 5–6. *Camptomeris verruculosa* (Syd.) Bessey

FIG. 5. Three sporodochidia from top view. About × 200
FIG. 6. Single sporodochidium from edge view. About × 200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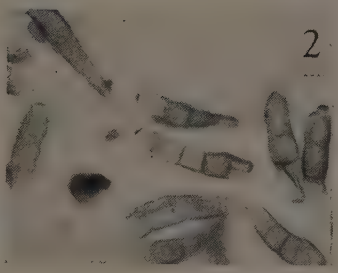
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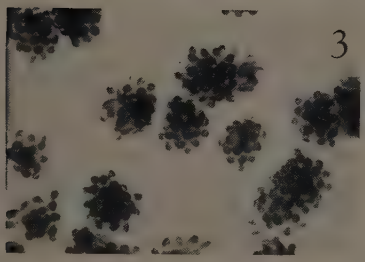
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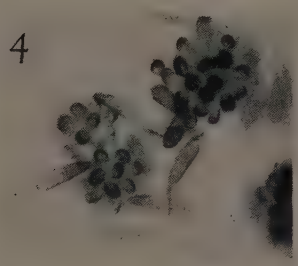
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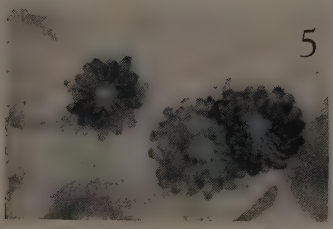
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Papers of the Michigan Academy of Science, Arts, and Letters,
Vol. XL, 1955 (1954 Meeting)

TAXONOMIC STUDIES IN THE GENUS LEUCOSTOMA

HEINZ KERN

Introduction

MODERN studies on the taxonomy of the Pyrenomycetes have led to considerable changes in the old classification of orders, families, and genera within this large and heterogeneous group of fungi (see Luttrell, 1951; Gäumann, 1952). Many of the old taxonomic units have been split and separated on the basis of new criteria (perithecial centrum, ascus structure, and so on). This process is still going on and is far from being completed; many more genera and species need to be studied in detail to give a solid basis for a better taxonomic and phylogenetic arrangement of these forms.

In the stromatic Pyrenomycetes (Diatrypaceae, Diaporthales, and the like), the genera Diaporthe, Melanconis, Pseudovalsa, and others have been revised by Wehmeyer (1933, 1941). For many other genera no monographs are available; numerous species have been described, but they need critical revision based on comparative studies and clearer species concepts. Work in this direction has been started by Défago (1935, 1942) in connection with species of Valsa and Leucostoma. The present paper reports on similar studies by me. It was thought that a comparison of American and European specimens of the same species in regard to their morphology, physiology, host range, and other aspects might lead to a broader basis for a future systematic treatment of the group and might give some additional information about the behavior of plant pathogenic fungi of one continent when introduced into another.

The specimens were collected during the summer of 1953 in southern and northern Michigan. The work was begun in the Botany Department and the Biological Station of the University of Michigan and continued in the Department of Applied Botany at the Swiss Federal Institute of Technology in Zurich.

I wish to express my gratitude to the Swiss Foundation for biological and medical fellowships that made my stay in the United States possible. My sincere thanks are also addressed to Dr. A. H.

Smith, Dr. F. K. Sparrow, and Dr. L. E. Wehmeyer, and to all my friends in Ann Arbor and elsewhere for their interest and helpful assistance during my visit. Through the kindness of Dr. D. P. Rogers I had the opportunity to examine herbarium specimens from the New York Botanical Garden. Finally, I wish to thank my wife for her coöperation during these studies.

Methods

The delimitation of species within this pyrenomycetous group of fungi is rather difficult. The aspect of the fructifications, the size and structure of the stroma, and similar details depend to a great extent on the bark anatomy of the host; it is therefore in many cases hard —or impossible—to decide which characteristics of a particular specimen are stable and which ones are variable. The problem is further complicated by the fact that the conidial stages frequently occur alone, so that a connection with a perithecial stage may not be established. To clarify these relations and to ascertain the variability of a given fungus, pure culture studies have been carried out by different authors (see Wehmeyer, 1930; Défago, 1935; Steven, 1935), partly in connection with inoculation experiments on different hosts. For a better knowledge of these fungi, biological studies of the host range and of variation in many strains are needed. On the basis of these investigations the older and, often, scarcely known species must be revised. There are three possible courses to follow:

1. Morphological examination of the specimens collected;
2. Studies on the behavior in pure culture;
3. Inoculation experiments on different hosts.

The present paper deals mostly with morphological studies. In particular, the taxonomic value of the spore size has been examined. Ascospores and conidia are very small in most species and have to be measured very carefully. Satisfactory results were obtained with spore smears in India ink by making direct measurements, or measurements of camera-lucida drawings, of 100 or 200 spores. For the statistical evaluation, the formulas of Linder (1951) were used.

Taxonomy and Phylogeny of the Genus Valsa Fr.

The genus Valsa as founded by Fries (*Summa veg. Scand.*, 2: 410. 1849) comprised a large number of stromatic Pyrenomycetes

with hyaline or brownish, allantoid (sausage-shaped) spores. Later studies showed that different types of perithecial development and structure had been brought together in this genus; consequently it was divided into smaller groups (Nitschke, 1867; Saccardo, 1882; Winter, 1887; Ellis and Everhart, 1892; and others). After elimination of Eutypa, Eutypella, Cryptosphaeria, and so on, there remained in the genus the closely related subgenera Euvalsa, Leucostoma, and Valsella. They are ranged today in the order Diaporthales and are characterized by the "Diaporthe centrum" (Wehmeyer, 1926; Luttrell, 1951, p. 50), by short-stalked asci with a refracting apical ring, and by hyaline spores. As in many other groups of fungi, the details of development and the structure of the fruiting bodies need much more study.

As proposed by von Höhnel (1917), it seems best to give these subgenera the rank of genera, and to arrange them in the following way:

1. Fructifications surrounded by a black basal zone, the conceptacle
   2. Asci with 4 or 8 spores ..... Leucostoma Nit. sensu stricto
   2. Asci with many spores ..... Valsella Fuck.
1. No black basal zone present ..... Valsa Fr. sensu stricto (syn. Euvalsa Nit.)

In the pages that follow, the characters of some better-known Leucostoma species and their relations are discussed.

Some Leucostoma Species

The Genus LEUCOSTOMA Nit. sensu stricto, Pyrenom. Germ., p. 221. 1867 (as subgenus)

Stromata surrounded by a black zone, the conceptacle, which contains either perithecia or pycnidia, or both. Asci short-stalked, with a thickened wall and a refractive ring at the apex, 4- or 8-spored. Ascospores and conidia hyaline, allantoid. The conidia are produced in a simple, irregularly chambered pycnidial cavity, which is formed either in the center of a perithecial stroma or alone in a stroma (Cytospora Ehrenb. or Leucocytospora v. H.) and usually opens by one central pore, through which the conidia are pressed out in long threads.

1. *Leucostoma persoonii* (Nit.) v. H., Mitt. Bot. Inst. Techn. Hochsch. Wien, 5: 60. 1928

Sphaeria leucostoma Pers., Usteris Annal. Bot., 2: 23. 1795.
Sphaeria leucostoma Fr., Syst. myc., 2: 387. 1822.
Valsa leucostoma Fr., Summa veg. Scand., 2: 411. 1849.
Valsa persoonii Nit., Pyrenom. Germ., p. 222. 1867.

Stromata generally numerous, scattered, rounded to irregular or elliptical, reaching 3 mm. in diam., not at all, or only slightly, prominent on the outside, sometimes uniformly gray, sometimes divided

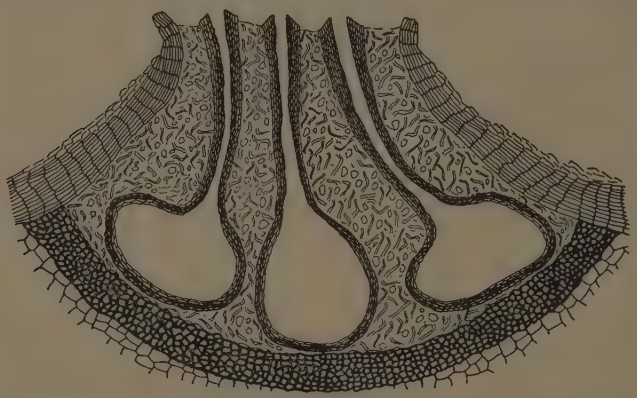

Fig. 1. Simplified section through a fructification of *Leucostoma persoonii*. The perithecial stroma is surrounded by the black conceptacle; the numerous, small asci which fill the whole perithecial cavity are not shown. About × 50

into a gray ectostroma and a brownish entostroma, surrounded by the black conceptacle, 100–250 μ thick, which sticks to the inner surface of the periderm; ascostromata without a central pycnidium. Disc erumpent in the center of the stroma through cracks in the periderm, truncate, 0.1–0.3, sometimes up to 0.5 mm. high, rounded or angular to elliptical, transversely elongated (depending on the bark structure of the host), in general 0.5–1 mm. in diam., occasionally reaching 2 mm. in length, pure white, seldom gray; ostioles 5–12 (20), globose-flattened, black, irregularly scattered on the disc or rather circinate. Perithecia globose to irregular with long, slender necks, about 150–700 μ in diam., scattered or circinate.

Asci clavate, 8-spored, 35–55 × 6–10 μ. Ascospores hyaline, allantoid, mostly 8–14 × 1.5–3 μ. (See Fig. 1.)

Stromata of the conidial form (*Cytospora leucostoma* Sacc.) similar, generally smaller than the ascostromata (1–1.5 mm. in diam.). Disc small, white, mostly with one black pore in the center. Pyc-

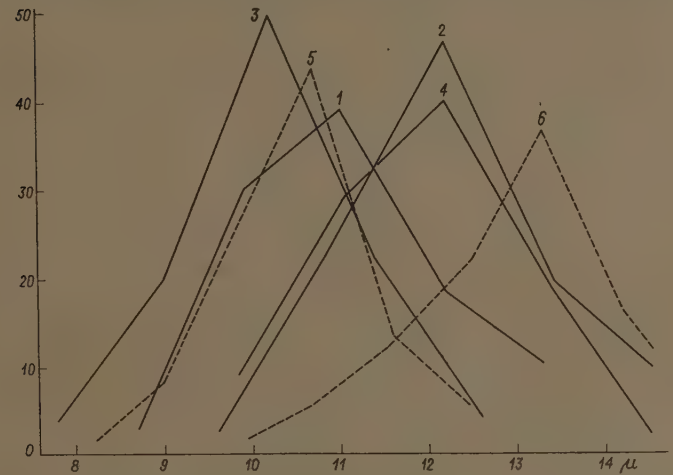

Fig. 2. Distribution of ascospore length in different strains of *Leucostoma persoonii* (100 spores each): 1, on *Prunus avium*, Ann Arbor, Mich.; 2, on *P. insititia* (?), Ann Arbor; 3, on *P. serotina*, Quincy, Ill.; 4, on *P. serotina*, Ann Arbor; 5, on *P. armeniaca*, Charrat, Switzerland; 6, on *P. mahaleb*, Charrat, Switzerland. (Nos. 3 and 4 collected by L. E. Wehmeyer; 5 and 6 after Défago, 1935.)

nidial cavity irregularly folded or chambered, occasionally simple. Conceptacle black, thick. Conidia allantoid, hyaline, 4–6.5 × 0.5–1.5 μ, pressed out in dark-red threads.

This is a very common fungus which occurs mostly on different species of Prunus (*P. avium*, *P. cerasus*, *P. serotina*, *P. insititia*, *P. americana*, *P. pennsylvanica*, and others), Sorbus, and related genera. It is easily recognized by its pure-white, flat, smooth disc, which becomes free through cracks in the periderm; the edge of the stroma is not visible from the outside, and the conceptacle is closely adnate to the inner side of the periderm.

The species was studied by Leonian (1923) in North America, by Togashi (1930a, 1930b) in Japan, and by Défago (1935) in Europe. Défago compared numerous specimens from different hosts and localities. He came to the conclusion that the species may be maintained as such, but that it consists of many individual races. These races show minor morphological differences (for instance, in

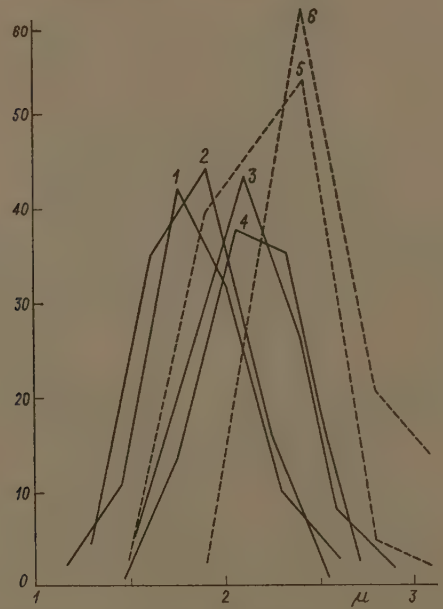

Fig. 3. Distribution of ascospore width in different strains of *Leucostoma persoonii*. The strains are the same as in Figure 2.

spore size), and they also differ considerably in their behavior in pure culture and in their pathogenicity for various hosts.

The situation is the same for the American strains. The species cannot be split up on the basis of morphological characteristics, for there is a certain range of variability in the parts which are not in direct connection with the bark tissue of the host. When more specimens from other regions have been examined, this range may become still wider and the species limits even less sharp. The dis-

tribution of ascospore length and width in different strains of this species may be seen in Figures 2 and 3; the conidial distribution would present a similar picture.

Pure cultures of these strains show specific characteristics in growth, in pigment formation, in the size and number of fructifications, and so on. Different strains, and sometimes even different single-spore isolates from one strain, may be distinguished from each other in culture. At the border line between some of the isolates, peculiar stromatic bodies occur, as reported for many other fungi by previous investigators. These details of metabolism and the host-parasite relations will be studied by me in future experiments.

2. *Leucostoma cincta* (Fr.) v. H., Mitt. Bot. Inst. Techn. Hochsch. Wien, 5: 61. 1928

Sphaeria cincta Fr., Syst. myc., 2: 387. 1822.
Valsa cincta Fr., Summa veg. Scand., 2: 411. 1849.

Stromata rounded or elliptical, 2–4 mm. in diam., definitely prominent, conical, with an externally visible outline, generally divided into a gray ectostroma and a brownish entostroma which contains the remains of the host tissues; conceptacle black, 20–100 (150) μ thick, closely adnate to the inner bark tissues. Disc rounded, angular or elongated, reaching 2 × 1 mm., mostly convex, dirty pale gray or brown-gray; ostioles 5–12 or more, globose-flattened or elongate, usually circinate around a central pycnidial pore. Asci clavate, 8-spored, 45–80 × 7–15 μ. Ascospores hyaline, allantoid, mostly 8–20 × 2–4 μ.

Stromata of the conidial form (*Cytospora cincta* Sacc.) similar. Pycnidium simple or radiate-chambered. Conidia allantoid, hyaline, 5–8 × 1–2 μ.

This species occurs on twigs of Prunus (*P. armeniaca*, *P. spinosa*, and others), Amelanchier, and related hosts. It was not found in Michigan during the summer; only herbarium specimens were examined by me. The fructification of this species may resemble that of *Leucostoma persoonii*, but it differs in several respects: the disc is dirty brown, the stroma is more conical, and a pycnidium is often present in the center of an ascostroma. The conceptacle is rather thin and remains with the bark parenchyma when the periderm is removed.

The ascospores vary to a great extent. Many European strains have big spores (Défago, 1935: average 15.8–17.5 × 3.1–3.3 μ); the spores of a specimen (Sand Coulee, Montana) mentioned by Ellis and Everhart measured 14.3 × 3.3 μ; another specimen, from Ontario, had spores measuring 11.8 × 2.4 μ. These spores fall into the range of *Leucostoma persoonii*. Their other characteristics seem to permit a clear separation of the two species, but the possibility remains that intermediate forms are to be found and that the typical specimens of these species represent the extremes of one series.

3. *Leucostoma nivea* (Fr.) v. H., Mitt. Bot. Inst. Techn. Hochsch. Wien, 5: 58. 1928

Sphaeria nivea Hoffmann, Veg. crypt., 1: 26. 1787.
Sphaeria nivea Pers., Synop. fung., p. 38. 1801.
Sphaeria nivea Fr., Syst. myc., 2: 386. 1822.
Valsa nivea Fr., Summa veg. Scand., 2: 411. 1849.

Stromata usually numerous, covering large areas of dead twigs and stems, rounded, 1–2 mm. in diam., slightly prominent and erumpent in the center, generally divided into a light-gray, powdery ectostroma and a gray-brown entostroma; conceptacle black, mostly 50–100 μ thick, convex, adnate to the inner surface of the periderm, often continuing on the upper side of the stroma and blackening the bark surface around the disc. Disc truncate, 0.2–0.5 mm. high, rounded, angular or elongate, 0.3–1 mm. in diam., snow white to pale brownish, often powdery; ostioles 3–12, black, globose-flattened, circinate, irregularly scattered, or clustered as a black spot in the center. Perithecia globose to irregular with slender necks, 200–600 μ in diam., circinate or scattered, sometimes with a central pycnidium. Asci clavate, 4- or (mostly) 8-spored, 30–60 × 5–10 μ. Ascospores allantoid, hyaline, about 7–15 × 1–3 μ (Figs. 4–5).

Stromata of the conidial form (*Cytospora nivea* Sacc.) similar, with a rather small, brownish-white disc, a radiate-chambered pycnidial cavity, and generally one central black ostiole. Conidia allantoid, hyaline, 4–7 × 0.8–1.5 μ.

This very common species is widely distributed on twigs and stems of poplars and aspens (*Populus alba*, *P. balsamifera*, *P. nigra*, *P. tremuloides*, *P. tremula*, and others). Its numerous, snow-white discs with black ostioles are most conspicuous. Typical, well-developed fructifications differ from those of *Leucostoma persoonii* in

the powdery consistency of both disc and stroma, and in the conceptacle, which generally forms a black line surrounding the whole surface of the stroma except the disc. The specimens which have so far been studied in North America and in Europe correspond in all their characteristics except spore size. Ellis and Everhart discovered as early as 1892 that the ascospores of strains found in

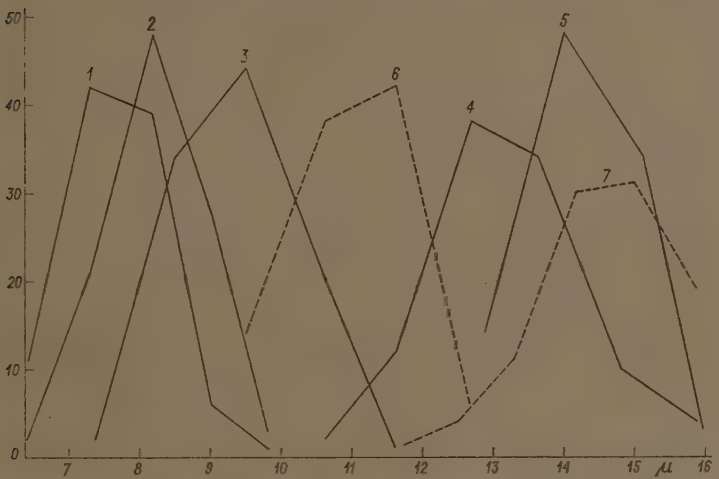

FIG. 4. Distribution of ascospore length in different strains of *Leucostoma nivea* (100 spores each): 1, on *Populus alba*, Ann Arbor, Mich.; 2, on *P. tremuloides*, Mackinaw City, Mich.; 3, on *P. tremuloides*, Madison, Wis.; 4, on *P. grandidentata*, Hubbardston, Mass. (collected by L. E. Wehmeyer); 5, on *P. tremuloides*, Isle Royale, Mich. (collected by A. H. Povah); 6, on *P. tremula*, Herblingen, Switzerland; 7, on *P. nigra*, Monthey, Switzerland (after Défago, 1935)

Colorado and Montana were considerably smaller than those measured by European investigators. Wehmeyer (1942) reported both small-spored and large-spored forms. In order to secure more information on this point, many specimens from Michigan and elsewhere were examined in the course of my investigation. At first, two distinct groups seemed to exist—one with small and one with large ascospores. Later, intermediate forms were found, and measurements of the spores of the strains now known cover, irregularly, a wide range (Figs. 4–5). Specimens with rather small spores were collected in many localities of southern and northern Michigan and

in other states; those with larger spores occur frequently in Europe but some also occur in North America (for instance, those collected by A. H. Povah on Isle Royale, Michigan).

A similar, but smaller, range of variation was found for the conidia. The relations between the perithecial and the conidial

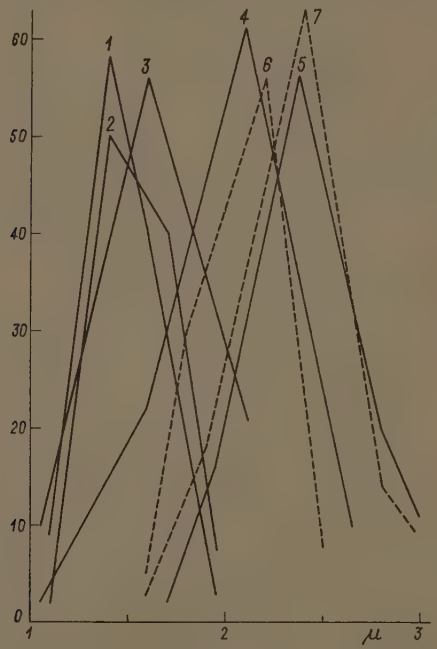

Fig. 5. Distribution of ascospore width in different strains of *Leucostoma nivea*. The strains are the same as in Figure 4.

stages are often difficult to establish; observations in nature have to be completed by experimental studies. Many forms with small ascospores (8 × 1.5 μ) were accompanied by small conidia (4.6 × 1 μ)—frequently on aspen in the Douglas Lake region, Michigan; and some strains with big spores (14 × 2.5 μ) had big conidia (6–6.5 × 1.3 μ). There were so many exceptions, however, that no general correlation was established.

A further character of the individual strains is their aspect in

pure culture (cf. Schreiner, 1931). The development on different media, the type and growth of the mycelium, the color of the spore horns, and the character of the stromata may be characteristic for

TABLE I

ASPECT OF SOME LEUCOSTOMA NIVEA STRAINS IN PURE CULTURE

Collection no.	Host and locality	Ascospores		Growth on malt-extract agar
		Length in μ	Width in μ	
621	*Populus alba*, Ann Arbor, Mich.	7.6 ± 0.7	1.5 ± 0.2	Mycelium appressed, olive black; some small, olive pycnidia; conidial masses orange-brown
661	*P. tremuloides*, Cibola Nat. Forest, N. M.	8.8 ± 0.7	1.9 ± 0.35	Mycelium appressed, white with yellowish-white aerial hyphae; big, light-gray pycnidia; pale-yellow masses of conidia
642	*P. tremula*, Herblingen, Switzerland	11.0 ± 0.9	2.1 ± 0.3	Mycelium olive black; some large, light-gray pycnidia; conidial masses orange-red
643	*P. tremula*, Thalwil, Switzerland	11.8 ± 1.2	3.4 ± 0.3	Mycelium white to pale yellow; pycnidia olive gray; conidial masses pale yellow

certain strains. Some examples are given in Table I. It is clear that light-colored and dark-colored strains occur, but no relationship between such coloration and the source of the strain or its spore size could be established.

4. *Leucostoma kunzei* (Fr.) Munk, Dansk Botanisk Arkiv, 15: 80. 1953

Sphaeria kunzei Fr., in Kunze and Schmidt, Mycol. Hefte 2: 45. 1823.
Valsa kunzei Fr., Summa veg. Scand., 2: 411. 1849.

Stromata generally numerous, covering large areas of twigs or stems, rounded to elliptical, 1–2 mm. in diam., prominent, conical on the outside, often with a clearly visible margin, sometimes flat-

tened or even depressed around the disc; substance pale yellow to light gray or brownish; conceptacle black, about 50–100 μ thick, more or less adnate to the inner bark tissues. Disc rounded to elliptical, flat or convex, erumpent, white to pallid, later brown, 0.2–1 (1.5) mm. in diam.; ostioles generally numerous (5–30), often crowded and covering the whole disc, black, small, globose-flattened or sometimes elongate. Perithecia globose to irregular with slender necks, about 200–600 μ in diam. Asci clavate, 15–25 $\times$ 4–6 μ. Ascospores hyaline, allantoid, mostly 5–8 $\times$ 1–2 μ.

Stromata of the conidial form (*Cytospora kunzei* Sacc.) similar, generally smaller, with, occasionally, a very thin conceptacle, and with radiate chambers and a central pore. Conidia allantoid, 4–6 $\times$ 0.5–1 μ.

This species was often collected on *Abies balsamea* in Northern Michigan (Emmet and Cheboygan counties; Tahquamenon Falls State Park) and elsewhere; the material corresponds well with that known from Europe on *A. alba*. The fructifications vary in aspect and size (small, conical or convex, with an uneven but definite outline); single ostioles sometimes grow very long. The conceptacle of the conidial form is sometimes very thin, but often it is rather thick and conspicuous. There seems no reason to exclude this species from Leucostoma, as was proposed by von Höhnel (1928). The host range is probably wider than it was originally believed to be. Material from other hosts such as *Pinus strobus*, *P. resinosa*, and *Tsuga canadensis* shows no real differences from that on Abies. *Leucostoma kunzei* was also reported on Picea by Marsden (1948). Other species recorded on conifers (i.e., *Valsa superficialis* Nit., on *Pinus strobus*) are probably the same as *L. kunzei*. Their taxonomic position needs further study.

Conclusion

From the foregoing evidence, it must be concluded that the main questions in the taxonomy of the genus Leucostoma are still open. It has been shown that the spore size within one species may vary over a considerably wider range than might be expected. Until the intermediate forms are found, extreme strains of one series may, therefore, appear to be different species. This fact, together with the variability of the stromatic parts under different external condi-

tions, with different host tissues and so on, makes difficult the delimitation of species on a purely morphological basis. In such a situation, biological criteria are needed to complement the morphological ones. To a degree, biological criteria have been utilized in the past, because most of these species were described as they appeared on certain host plants. In some cases (for instance, *Leucostoma persoonii* and *L. nivea*) the plants indicated are probably their principal, but not their only, hosts in nature. In other cases, however, a well-known fungus may appear in an aberrant form on a new host, and, as a result, may be described as new. (This is probably what happened with some species on conifers.) For the moment it seems advisable to maintain the present arrangement of the species of Leucostoma here discussed. In the meantime, experimental studies upon such questions as the physiology of individual strains and the degree of their pathogenicity on various hosts should lead to clearer concepts of the species and their subdivisions.

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SOME ENTOMOGENOUS SPECIES OF ISARIA*

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THE genus Isaria belongs in the Stilbaceae of the Fungi Imperfecti. As described by Fries (1829–32) it included species which are now known to differ considerably in microscopic characters. Fries grouped together and treated ten species on insects. Subsequently many other entomogenous species have been described. Most of the species which have been included in Isaria have one-celled, hyaline conidia produced on simple or branched synnemata. They differ considerably, however, in the structure of the synnemata and in the manner in which the phialides and spores are produced.

With the accumulation of information, the species of Isaria have been separated into several genera. In consequence, questions have arisen concerning the application of the name Isaria. Petch (1934) has stated that *I. terrestris* is the type of the genus, apparently because it is the first species treated by Fries under the genus in his *Systema mycologicum*, but he says that *I. terrestris* has not been collected since Fries reported it. Petch studied a slide from the type specimen and was unable to find phialides or spores. He concludes that the specimen is probably an immature hymenomycete, and that its identity cannot be established. Petch suggests the possibility of recognizing *I. farinosa* as the type of the genus. However, he thinks that *I. farinosa* is a compound species of Spicaria, and that the union of conidiophores into synnemata is of minor importance. He therefore concludes that it is simpler to discard the genus Isaria and to place *I. farinosa* and similar species in Spicaria. The information given by Petch excludes *I. terrestris* as a lectotype of Isaria, but the view that species of Isaria and Spicaria are congeneric does not justify the discarding of Isaria, since on the basis of priority it should be the name of the combined genera.

The application of the name Isaria depends upon the species which is chosen as the lectotype for the genus. On account of the

* Paper from the Herbarium and the Department of Botany of the University of Michigan.

diversity of species included by Fries, complete agreement may not be reached. Clements and Shear (1931) have proposed *I. farinosa* as the lectotype. This appears to be a good selection. The identity of *I. farinosa* is fairly certain from the description and illustration cited by Fries. It is a widely distributed and fairly common species on insects and one for which considerable information is available. The genus will therefore be discussed here with *I. farinosa* as the lectotype.

Whether the species of Isaria and Spicaria should be united in one genus is questionable. Both are genera of the Fungi Imperfecti and as such are based on conidial stages. The valid names for the species are those of the perfect stages if known, or will be those of the perfect stages when discovered. The species and their relationships also must be based mostly on knowledge of the perfect stages. Isaria and Spicaria are useful designations which represent conditions or states. A fungus may have both an Isaria and a Spicaria condition. If it is necessary to treat both under one name in the absence of a perfect stage, the name should be based on priority. In this paper, the genus Isaria is limited to the stilbaceous condition in which synnemata are produced. The following is a description of the genus.

ISARIA Fr., Systema mycologicum, 3: 270. 1829

Synnemata usually pulverulent, terete or compressed, simple or branched, consisting of bundles of more-or-less parallel, longitudinal hyphae; conidiophores, diverging outer hyphae of the synnemata or branches of the outer hyphae (Pl. I, Fig. 4), long, multiseptate, usually forming floccose masses on the upper portions of the synnemata; phialides ending short branches, which are grouped in terminal or lateral, more-or-less compact heads or whorls on the conidiophores; conidia hyaline, unicellular, catenulate.

LECTOTYPE.—*Isaria farinosa* Fr.

Many stilbaceous species on insects which were described as species of Isaria are now placed in Gibellula, Akanthomyces, Hymenostilbe, Insecticola, and Hirsutella. In these genera the conidiophores are not divergent and free above. The phialides are either sessile on the outer hyphae of the synnemata or on short lateral branches. Vera K. Charles (1941) in her check list of the ento-

mogenous fungi of North America gives twenty-seven species of Isaria. Of these, *I. farinosa*, *I. tenuipes*, *I. atypicola*, *I. cicadae*, *I. pattersonii*, and *I. dussii* are species of Isaria in the restricted sense. Collections of the first three have been available for this study, and descriptions follow. The other species in the check list are then discussed. The designations of the herbaria in which the specimens cited are deposited are those of the Index Herbariorum: BPI (Division of Mycology and Disease Survey, U. S. Bur. Plant Ind.); NY (New York Botanical Garden); NYS (New York State Museum); MO (Missouri Botanical Garden); MICH (University of Michigan).

Isaria farinosa Fr., Systema mycologicum, 3: 271. 1829

(Pl. I, Figs. 1–2)

Spicaria farinosa (Fr.) Vuill. ex Beauv., Rev. Gen. Bot., 26: 162. 1914.
Coremium swantonii A. L. Smith, Trans. Brit. Mycol. Soc., 6: 156. 1919.
Spicaria (*Isaria*) *swantonii* (A. L. Smith) Petch, Naturalist, 1931: 103.
Spicaria (*Isaria*) *farinosa* (Fr.) Petch, Trans. Brit. Mycol. Soc., 19: 38. 1934.

Synnemata few to many, usually crowded, simple, furcate or irregularly branched, light orange to yellowish brown, terete or somewhat compressed, up to 2 mm. thick below, consisting of more-or-less parallel hyphae 2–2.5 μ wide, with the upper portions of the synnemata white, floccose, and pulverulent from the spores; conidiophores diverging and becoming free from the synnemata for a considerable portion of their length, long, 1.5–2 μ wide, moderately septate, with short, ramose branches forming loose terminal and lateral heads or whorls; phialides 1–3 on the terminal cells of the branches, ovoid, 5–8.6 $\times$ 2.1–2.3 μ, hyaline, acute to acuminate above; conidia ellipsoid, 2.0–3.0 (4.2) $\times$ 1.5–2.1 μ, hyaline, catenulate.

On lepidopterous larvae: Michigan, A. H. Smith 26139 (MICH); Josiah Lowe (MICH); E. B. Mains 31–542 (MICH), 5100 (MICH); H. D. Thiers 794 (MICH). New York, Zaher (NY). Nova Scotia, L. E. Wehmeyer 384 (MICH). Pennsylvania, E. T. Reese (MICH). Washington, E. B. Mains 6203 (MICH). Virginia, C. L. Shear (BPI).

On a hornet: Michigan, A. H. Smith (MICH).

On undetermined hosts: Michigan, E. B. Mains (MICH). North Carolina, C. L. Shear (BPI).

Of the specimens studied, all the identified hosts were Lepidoptera except one, which was a species of hornet (Hymenoptera). Petch (1931c) has reported *Spicaria* (*Isaria*) *swantonii* on bees and wasps in England. He later (1936) included it in *I. farinosa*. The Michigan collection does not differ sufficiently from *I. farinosa* to justify separation as a species. When more is known concerning host specialization in this group it may be desirable to recognize it as a specialized race.

Isaria farinosa varies considerably. In some collections only a few synnemata occur. In others there are many, densely crowded. The size appears to be correlated to some extent with the size of the host. The extent of the branching is commented on by Fries in his treatment of the species.

The loose conidiophores and the catenulate conidia form white, floccose, pulverulent masses covering the upper portions of the synnemata. The conidiophores vary in the amount of branching. Petch (1936) states that the first conidiophores formed show less branching. In the fullest development the short lateral branches, with subbranches and terminal phialides, form heads or whorls which are terminal or at intervals on the conidiophores. Petch states that in culture the conidiophores are first produced directly from the mycelium. The fungus therefore may have both a Spicaria and an Isaria condition.

Atkinson (1894), Pettit (1895), and Petch (1936) have grown *Isaria farinosa* on various culture media without the production of an ascogenous stage. Tulasne (1857), DeBary (1884), Pettit (1895), and Shanor (1936) conclude from observations and cultures of *Cordyceps militaris* that the conidial stage is *I. farinosa*. Petch, however, obtained a species of Cephalosporium from cultures from ascospores of *Cordyceps militaris* and has questioned the connection with *I. farinosa*. Kobayasi (1941) has reached the same conclusions as Petch.

Isaria tenuipes Peck, Rep. N. Y. State Botanist, p. 49. 1879

(Pl. I, Figs. 3–4)

Synnemata few to many, simple or irregularly branched or furcate above, up to 35 mm. long, lemon yellow to light yellowish brown, terete or somewhat compressed, 0.5–1.0 mm. thick below, consisting of more-or-less parallel hyphae 2–2.5 μ wide, with the

upper portions of the synnemata white, floccose, and pulverulent; conidiophores long, free from the synnemata above, 2–3 μ wide, with short branches and subbranches forming terminal or lateral heads or whorls, moderately septate; phialides ovoid, 4–6 × 1.5–2.5 μ, acuminate above, 1–3 on the terminal cells of the branches of the conidiophores; conidia oblong or somewhat allantoid (3) 4–6.2 × 1.5–2 μ, hyaline, catenulate.

On lepidopterous pupae and larvae: Massachusetts, D. H. Linder and D. P. Rogers 2092 (NY). Michigan, B. O. Longyear (NYS); A. H. Smith 26150 (MICH). New Jersey, Ellis Coll. 1445 (NY). New York, Wm. S. Doty and D. P. Rogers 3101 (NY); D. P. Rogers 3099 (NY); Fred J. Seaver (NY); C. H. Peck, TYPE (NYS). Ohio, Lloyd Ellis Coll. (NY). Ontario, A. H. Smith 26306 (MICH). Pennsylvania, E. T. Reese (MICH). Tennessee, F. T. Wolf and W. T. Allman, Jr., 754 (MICH). Virginia, C. L. Shear (BPI); F. F. Dicke (BPI).

Isaria tenuipes is very similar to *I. farinosa*, from which it differs principally in having oblong, larger conidia. Vera Charles (1941) reports it only from New York. However, some of the specimens which have been identified as *I. farinosa* in herbaria are *I. tenuipes*. Petch (1942) has reported *I. tenuipes* from Europe. Evidently it has a fairly wide distribution.

Petch (1937) and Kobayasi (1941) have suggested that *Isaria tenuipes* is near *I. japonica* and *I. suffruticosa*. Kobayasi states that the conidia of *I. japonica* are cylindric and curved, and in his illustrations they are uniformly allantoid. Most of the conidia of the type of *I. tenuipes*, which was loaned by Stanley Jay Smith of the New York State Museum, are straight; only a few are slightly curved. The two species are very closely related. The description given by Petch of the type of *I. suffruticosa* indicates that it is probably the same as *I. tenuipes*.

Pettit has reported the development of *Isaria tenuipes* upon nutrient media. However, his illustrations show a fungus with spherical conidia produced in clumps on the sterigmata of the phialides. The species which he studied, therefore, was not *I. tenuipes*.

Isaria atypicola Yasuda, Bot. Mag. Tokyo, 29: 117. 1915

Synnemata usually arising singly from spiders within subterranean nests, simple, clavate, 1.5–3.0 cm. long; terminal sporogenous portions cylindric to clavate, up to 3 mm. wide, light

gray to purplish gray, pulverulent; stipes 1.5 mm. thick, light vinaceous to light brown; conidiophores long, mostly free from the synnemata, consisting of single, multiseptate hyphae 3–4 μ thick, having terminal and lateral clumps of short branches and phialides 25–40 μ in diameter; phialides subcylindric, 4–6.1 $\times$ 2 μ, acute above; conidia usually oblong, less frequently somewhat allantoid, 3.7–6 $\times$ 1.5–2 μ, hyaline, catenulate.

On trapdoor spiders: Costa Rica, Dodge and Goerger 9009, 9103 (MO).

Through the kindness of Carroll W. Dodge the specimens cited were loaned from the Herbarium of the Missouri Botanical Garden. They are those discussed by Petch (1939) and apparently are the only records of the species for North America. According to Kobayasi (1941), the species is fairly common in Japan.

Petch has suggested that *Isaria atypicola* is the conidial stage of *Cordyceps cylindrica*. This is only a surmise, since an association of *I. atypicola* with the ascogenous stage of *C. cylindrica* has not been observed. Furthermore, *C. cylindrica* was described by Petch (1937) from immature specimens in which asci and ascospores had not formed, and therefore the status of the species is uncertain.

Isaria cicadae Miq., on cicadas, has been reported for North America from Mexico and the West Indies, usually as *I. arbuscula* or *I. sinclarii*, which Petch (1933) regards as synonyms. The species has been described by Petch (1923, 1931a, 1933, 1942) and Kobayasi (1941), and the relation to a perithecial stage has been discussed. Petch reports specimens of *Cordyceps sobolifera* from Mexico which have branches on the perithecial clavae bearing conidiophores and conidia similar to those of *I. cicadae*, and he concludes that *I. cicadae* is the conidial stage of *C. sobolifera*. On the other hand, Kobayasi states that in Japan pycnidia are associated with *C. sobolifera*, and that *I. sinclarii* has not been found in association.

Isaria pattersonii was described by Massee (1912), who erroneously gives a scale insect as the host and the Gold Coast as the locality. Petch (1931b) has presented a description of the type, and states that it is on a pentatomid, *Nezera viridula*, from St. Vincent in the West Indies. The species appears to be very similar to *I. farinosa*.

Isaria dussii was described from Guadeloupe, on caterpillars, by

Patouillard (1900). Petch (1933) has supplied additional information concerning the species. He states that it is similar to *I. japonica* Yasuda and that it is the conidial stage of *Cordyceps polyarthra* Möller, but he does not present any evidence for the connection.

Although *Isaria dubia* Delacr. has not been found in North America, it should occur there on lepidopterous larvae, since Petch (1933) and Favre (1942) have reported it in Europe as the conidial stage of *Cordyceps gracilis* Mont. & Dur., which has been collected a number of times in North America (Charles, 1941; Mains, 1934, 1940). According to the descriptions given by Petch and Favre, the conidia are narrowly fusoid, 4–6 × 1 μ or 5–9 × 1–1.5 μ (Petch) or 3.5–7 × 1.3–2 μ (Favre).

As has been pointed out elsewhere (Mains, 1950b, 1951), *Isaria lecaniicola* Jaap on scale insects and *I. sphecophila* (Ditm.) Petch on wasps are species of Hymenostilbe; *I. barberi* Geard on lepidopterous larvae and *I. saussurei* Cooke and *I. crinita* Lloyd on wasps are species of Hirsutella. *I. arachnophila* Ditm. may be *Akanthomyces aranearum* (Petch) Mains. Petch (1932) considers *I. aspergilliformis* Rostrup to be the same as *Gibellula arenareum* Syd. (= *G. pulchra* (Sacc.) Cavara). *I. densa* Fr. was transferred to Beauveria by Vuillemin (1912). *I. vexans* Pettit is considered by Petch (1924) to be a form of *Beauveria globulifera* (Speg.) Pec. Judging by the descriptions and illustrations given by Lugger (1895), *I. tomicii* is also a species of Beauveria. *I. destructor* Metsch. is *Metarrhizium anisopliae* (Metsch.) Sor., according to Petch (1931a). *I. brachiata* Fr. is *Tilachlidium pinnatum* Preuss, which occurs on a number of species of fungi; it is probably a parasite of entomogenous fungi rather than of the insects on which they have been collected (Petch, 1937).

Isaria ritchiei was illustrated but not described by Lloyd (1919). It is a fungus on small Melolanthae from Jamaica. Through the kindness of John A. Stevenson, the specimen (No. 42602 in the Lloyd Herbarium of the U. S. Bureau of Plant Industry) was loaned for study. The larvae bear what appear to be immature clavae of a species of Cordyceps. They are cylindric, up to 35 mm. long and 0.7–1.5 mm. thick, tapering above to acute apices. They are light brown, with irregular coverings of thin, white, floccose mycelium on the upper parts. The phialides, which are obclavate, 10–16 × 2–2.5 μ, and acuminate, are irregularly scattered on the hyphae.

They bear more-or-less spherical (10–38 μ), agglutinated clumps of conidia. The conidia are subcylindric, 7–12 $\times$ 1.5 μ, more-or-less acuminate below, and hyaline. The fungus is therefore not a species of Isaria. It appears to be a species of Cephalosporium which has developed on the immature clavae of a species of Cordyceps.

The other species of Isaria listed by Miss Charles for North America are doubtful. *I. aranearum* Schw. is considered by Petch (1932) to be a species of Gibellula. However, as has been noted elsewhere (Mains, 1950a), the type is not in the Schweinitz Herbarium, and the application of the name is uncertain. *I. crassa* Pers. has generally been considered to be a synonym of *I. farinosa*, although the fungus cannot be accurately identified (Petch, 1931b). There is no specimen of *I. floccosa* in the herbarium of Fries, and the identity of the species is uncertain (Petch, 1933). The type of *I. furcata* Schw. occurs in the Schweinitz Herbarium, and through the kindness of Walter M. Benner and Ruth Patrick fragments of synnemata have been available for study. Conidiophores and phialides were not found, and the synnemata appeared to be overgrown by the brown mycelium of another fungus. The identity of the species is therefore doubtful. *I. gigantea* was described on a spider, *Mygale cubana*, from Cuba by Montagne (1838–42), and his description is not sufficient to identify the fungus. Nor can *I. nigripes* be determined from the description given by Schweinitz (1834). *I. sphingum* Schw. has usually been applied to a species of Akanthomyces (*A. aculeata* Leb.), but, as is indicated elsewhere (Mains, 1950b), its identity cannot be determined from the type in the Schweinitz Herbarium.

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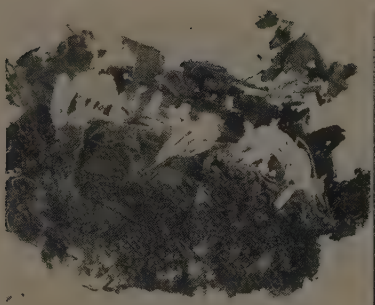
EXPLANATION OF PLATE I

Figs. 1–2. *Isaria farinosa*, Thiers 794

Fig. 1. Synnemata arising from a buried lepidopterous pupa. × 0.8
Fig. 2. Synnemata showing branching. × 3

Figs. 3–4. *Isaria tenuipes*, A. H. Smith 26150

Fig. 3. Synnemata from lepidopterous pupa. × 3
Fig. 4. Portion of synnema showing branching and free conidiophores with clumps of branches, stained with acid fuchsin. × 70



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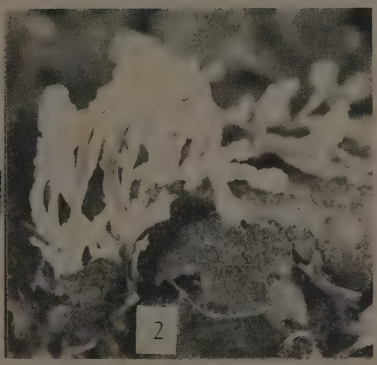

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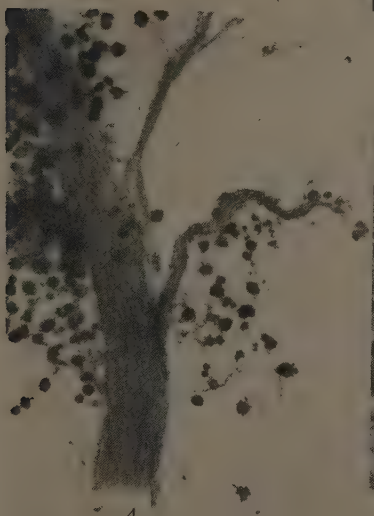

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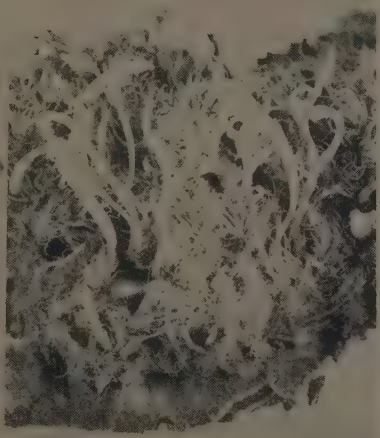

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THE STRUCTURE AND DEVELOPMENT OF THE CARYOPSIS IN SOME INDIAN MILLETS

V. *ELEUSINE CORACANA* GAERTN.*

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THE anatomy and embryology of the grasses afford stimulating subjects for study in view of the variety of forage and food plants included under the tribes, genera, and species. The investigations on Saccharum (3), Zea (7, 19, 28, 34), Oryza (13), Hordeum and Secale (6, 18), and Poa (2, 26, 27, 30), among others, have amplified our knowledge in many important details. Avery (5) and McCall (17) have presented a comparative account of the anatomy and morphology of the embryos of Zea, Avena, and Triticum.

A perusal of the literature on the embryology of the millets indicated, however, that adequate work had not been done on these plants, especially on the various phases of embryo development. Investigations of some cultivated Indian forms belonging to the tribe Paniceae were therefore undertaken, along with one on *Eleusine coracana* Gaertn., the finger millet, of the tribe Eragrosteae. A study of the structure of the embryo of *E. coracana* appears in the classical work on the grasses by Kennedy (14). Cummins (8) later reported on *E. indica*, and Krishnaswamy and Ayyangar (16) on *E. coracana*. Khosla (15) has made a few comparative observations on four Indian millets, of which *E. coracana* is one. A consideration of the method of formation of pollen and of the male gametophyte in the plant has been published by me elsewhere (20). The present paper deals with the embryology of the species, beginning with sporogenesis and culminating in the formation of the mature grain.

Material and Methods

For the purpose of this study, seeds of *Eleusine coracana* were obtained through the Millet Specialist, Department of Agriculture,

* The work reported in this paper was done at the University of Delhi, India. The author is at present attached to the Department of Botany, University of Michigan, as a Fulbright scholar.

Madras, India, and sown at the University Botanical Garden, Delhi, India. Young spikelets were fixed in the field in formalin-acetic-alcohol, and for postfertilization stages the ovaries were dissected out. Dehydration and embedding were done by the customary methods, with xylene as the clearing agent. Sections were cut 10–15 μ thick and were stained either with safranin and fast green or with Haidenhain's iron-alum hematoxylin.

Detailed Observations

floral organs

The rachilla of the spikelet of *Eleusine coracana* has a zigzag shape and usually bears six florets, one at each bend or node (Pl. I, Fig. 1). The uppermost flower is reduced or abortive. The outer pair of glumes is sterile. Each floret is enclosed by the lemma and the palea, whose internal structure closely resembles that of the grass leaf.

The lemma is five-nerved. In cross section it shows a V-shaped outline and a prominent median vascular bundle with two smaller ones adjacent (Pl. I, Fig. 2). The two lateral strands are conspicuous only at the base. The vascular bundles are collateral and endarch, and are surrounded by a sheath of sclerenchymatous cells. Around the periphery of the central bundle is a band of large chloroplast-containing cells that form a sheath (Fig. 3). The plastids are distributed sparsely over the rest of the mesophyll. Stomata are present on both sides. The epidermal layers are cuticularized, as are the guard cells.

The palea is typically bikeeled and is smaller than the lemma. In the region of the two keels the tissue is prolonged backward in the form of membranous wings. At the center of the broad base is a groove into which fit the margins of the lemma of the next floret (Pl. I, Fig. 4).

The lodicules are trapezoid in shape and are traversed by a number of procambial strands, but by no lignified elements. Neither chloroplasts nor stomata are present. The three stamens arise at the same level, just below the ovary. Each filament contains a single vascular strand embedded in parenchyma. The number of xylem elements is reduced to one or two. The ovary is spherical and ends in two styles which bear plumose stigmas. Plate I, Fig-

ure 4, shows a cross section of the spikelet at the level marked 4 in Figure 1.

MEGASPOROGENESIS AND EMBRYO SAC FORMATION

At first the solitary ovule is erect, but the differential growth of the nucellus causes it to become campylotropous at the time the embryo sac is formed (Pl. I, Figs. 5, 8, 14). There are two integuments, each two-layered.

The hypodermal archesporial cell is terminal to an axial row of nucellar cells (Pl. I, Fig. 5). The ovule is atropous at this stage, and the two integuments are already differentiated. The single archesporial cell cuts off no wall cells and it directly becomes the megaspore mother cell (Fig. 6). The nucellar epidermis may remain single or may undergo a periclinal division, so that the tissue above the embryo sac becomes two-layered. Meiosis in the megaspore mother cell proceeds normally and gives rise to a linear tetrad of megaspores (Figs. 7–8). The upper three megaspores degenerate in basipetal succession, while the innermost is functional. The degenerated megaspores persist for a time as darkly stained streaks with flattened tops.

The functional megaspore enlarges progressively during development. By three successive divisions, an eight-nucleate embryo sac is formed (Pl. I, Figs. 9–11). The egg apparatus is typical. The two synergids are pyriform; each contains a small elliptical nucleus toward the upper end, near the cell wall, but no vacuoles. They have sharp-pointed beaks and lateral hooks, but the filiform apparatus is not pronounced. With the maturation of the embryo sac, the cytoplasm in the apical part of the synergids shrinks, and the synergids begin to degenerate at the time of entry of the pollen tube.

The egg cell is more or less spherical. Its nucleus is centrally placed, and the cytoplasm is alveolar. The egg lies between the synergids and extends slightly below them.

The pair of polar nuclei lies in the immediate vicinity of the egg. The nuclei do not ordinarily fuse until after fertilization, but earlier fusion to form the secondary nucleus was observed in one instance. Small starch grains are often found in the general cytoplasm of the embryo sac.

The antipodals typically number three and are the most con-

spicuous cells in the embryo sac. They are always uninucleate and have dense cytoplasm. Normally they appear to be of the glandular or secretory type, acting as reservoirs of food material. Occasionally they have pointed ends and they may also have a haustorial function (Pl. I, Fig. 12). Rarely, they become aggressive, one or more cells dividing further (Fig. 13). In some embryo sacs the antipodals simulate the egg apparatus in size, shape, and organization (Fig. 11). They are often found in an advanced state of degeneration before fertilization.

FERTILIZATION AND EMBRYOGENY

A single pollen tube penetrates the micropyle and enters the embryo sac between the cells of the nucellar epidermis. It grows between the outer integument and the ovary wall and comes to lie in close proximity to the egg cell. The two sperms are discharged in this position. Syngamy and triple fusion occur simultaneously (Pl. II, Fig. 15). A crescent of black granules (X bodies) is formed between the egg and the two polar nuclei. Frequently the male gamete fuses with only one of the polar nuclei even when they are in close contact with each other. Fusion of the two nucleoli occurs soon after fertilization.

The zygote does not divide immediately, but undergoes a period of rest, during which a large number of endosperm nuclei are formed. Plate II, Figure 16, shows the zygote and a peripheral layer of free nuclear endosperm. The first division of the zygote is transverse (Figs. 17–18). The resulting terminal cell *a* is smaller than the basal cell *b*. The latter divides transversely to give rise to cells *c* and *d* (Fig. 19). The terminal cell *a* next divides vertically so that a four-celled proembryo is formed (Fig. 19). Transverse divisions follow immediately in the two basal cells (Fig. 20) and result in the formation of two cell tiers, viz., *e*, *f* and *g*, *h* (Fig. 21). A vertical division at right angles to the first one occurs in the terminal pair of cells, producing quadrants; further divisions, also vertical, follow in the cells *e* and *f*, which lie next to the terminal cells (Fig. 22).

The cell *h* (Pl. II, Fig. 21) forms the suspensor initial and, by a series of transverse divisions, gives rise to a row of suspensor cells (*i*, *j*, *k*, and *l*) as shown in Figure 23. When embryo differentiation takes place, the suspensor is eight to nine cells in height and two to three cells broad (Figs. 24–25). Periclinal divisions in the tiers *a*

and *e* cut off the dermatogen. Figure 26 shows a cross section of the proembryo at the stage indicated in Figure 23. At the time of differentiation of the plerome, periblem, and dermatogen, the embryonal mass is seven or eight cells wide.

The coleoptile is differentiated as a ridge of tissue ensheathing the growing point on the germinal face of the embryo. The coleoptile lip that arises above the vegetative cone apparently develops more rapidly than the lip beneath it (Pl. II, Fig. 27). The concentric edges of the bulge unite to form the coleoptile. Figure 27 shows the differentiation of the various organs of the embryo. As this differentiation progresses, the upper and the lower parts of the scutellum enlarge and expand laterally into two wings. The epidermal layer of the scutellum in contact with the endosperm consists of columnar cells that form an epithelium. As the embryo matures, the cell walls of the scutellum above the coleoptile and below the coleorhiza seem highly cutinized.

In the lower part of the embryo a cleft, resulting from the disintegration of a layer of cells around the radicle, separates the radicle proper from the outer tissue which forms the coleorhiza. A root cap develops through the activity of a calyptrogen layer between the tip of the root and the root sheath.

The epiblast appears as part of the coleorhiza. In longitudinal sections its tip almost reaches the apex of the coleoptile. It contains no vascular trace. A longitudinal section of the mature embryo is represented in Plate II, Figure 28.

The grain is oblong to globose, dark brown in color, and lies free between the lemma and the palea. It is slightly flattened on one side and shows a black hilum. The mature embryo lies at the base of the caryopsis. It is bent like a horseshoe, the epiblast forming a protective covering. The radicle appears to be almost at right angles to the longitudinal axis of the fruit, and the insertion of the scutellum is not very close to the plumule sheath. The vascular trace does not reach the apex of the scutellum. The ligular process on the portion of the scutellum above the coleoptile is small, but easily seen.

The mature embryo has a procambial system but no mature vascular elements. In cross section the root shows five to six protoxylem initials around the central metaxylem vessels of wider lumen (Pl. II, Fig. 29). A cross section through the nodal plate shows the

transverse-running procambial strands arranged in two groups. The larger group is U-shaped and comprises three subgroups. The subgroup at the base of the U extends to the scutellum and forms the scutellum trace, while the two flanks ascend as coleoptile traces (Fig. 30). The median trace formed above the node is smaller than the combined coleoptile and scutellum groups. It breaks up into several smaller strands at the base of the coleoptile node. These strands run obliquely outward and effect the vascularization of the primary leaf (Fig. 31). Short lateral traces are formed by the scutellum bundle. Stomata occur on the upper surface of the coleoptile (Fig. 32), but since there are no subsidiary cells adjoining the guard cells and no conspicuous air space beneath them, they are probably rudimentary and nonfunctional.

ENDOSPERM

Plate III, Figures 33–38, shows the developmental history of the endosperm, nucellus, integuments, and pericarp. The primary endosperm nucleus divides soon after the occurrence of triple fusion. Five successive nuclear divisions, resulting in the formation of thirty-two free endosperm nuclei, intervene before the zygote divides. These nuclei are distributed on the periphery of the embryo sac by vacuolation at the center. Sixty-four nuclei are present when the proembryo is bicellular, and about eighty-four at the four-celled stage. The nuclei are seen in pairs, embedded in dense cytoplasm. The entire cavity of the embryo sac is filled progressively, as more and more nuclei are formed. Cell-wall formation occurs first in the region around the eight-celled proembryo. The changes involved in the endosperm, nucellus, integuments, and in the pericarp during the growth of the ovule are shown in Figures 33–34. The endosperm occupies the entire space inside the ovule and is bounded only by the epidermis. In later stages, cell division is confined to the peripheral zone, and regular radial rows of endosperm cells develop toward the inner region (Fig. 37). The cells near the center and the crown ends are larger and are polygonal.

The outermost layer functions as the aleurone. Starch grains are deposited in all cells except those which constitute the aleurone layer. The cells of this layer are small and appear rectangular in longitudinal and cross sections. Each cell contains an ovoid nucleus and aleurone grains embedded in cytoplasm. The cell walls are

strongly cutinized. Normally the aleurone is a single layer, but in the fully mature caryopsis it may appear double in certain places (Pl. III, Fig. 38). Occasionally, involution of the aleurone layer occurs through the middle of the kernel (Fig. 39).

The cells of the endosperm which line the funiculus are more-or-less elongated and are devoid of starch grains. The hilar orifice (Pl. II, Fig. 27, *hi. or.*) forms a dark pad consisting of rows of glandular cells which make a kind of tapetum (*tp.*) in contact with the endosperm. The cells of the tapetum are highly protoplasmic and perhaps function as a transmitting tissue.

Other changes follow endosperm development. The synergids are completely resorbed. The antipodal cells do not retain their terminal position, but become laterally displaced (Pl. II, Fig. 16). These cells are densely protoplasmic and sometimes show chromatic bodies in the cytoplasm. With the expansion of the endosperm, however, they are laterally compressed and finally obliterated. The suspensor, which was a distinct organ of the embryo, also disorganizes at maturity.

FRUIT

Nucellus.—The nucellus is single-layered in the micropylar region but it is composed of two to three layers on the sides and of four to five layers toward the antipodal end of the embryo sac. The cells are rectangular and parenchymatous. As progressive expansion of the endosperm occurs, the cells of the nucellus are consumed, leaving only the nucellar epidermis. This collapses, also, at the time when starch grains are about to be deposited in the endosperm cells. In the mature caryopsis it is completely obliterated.

Testa.—As mentioned before, the ovule has two integuments, both of which are two-layered. Occasionally, however, the outer integument may show three cell layers in its insertion region above the funiculus. The cells of the outer integument are of uniform size and are elongated in the direction of the axis of the ovule. The outer integument may approach, but does not grow over and cover, the micropyle. Signs of its disorganization are apparent soon after fertilization occurs, and it is completely collapsed at the cellular phase of the endosperm. Only faint vestiges of the cell walls remain, closely adhering to the pericarp, and even these are obliterated in later stages.

The cells of the inner layer of the inner integument are radially elongated and are twice the size of those of the outer layer. These cells become greatly enlarged, and brown deposits, probably tannin, begin to appear in both the cell layers. The outer tangential wall of the outer layer becomes highly convex and presents an undulating appearance. It is thickened by the deposit of cellulose and is distinctly lamellate. Its outer surface is strongly cutinized (Pl. III, Fig. 38). The lumina of the cells become considerably narrowed and may contain brown deposits. Thus both the cell layers of the inner integument persist in the mature caryopsis.

Pericarp.—At the time of embryo-sac formation, the pericarp is composed of seven to eight layers on the micropylar side; it is slightly thicker on the stylar side. A dense deposit of starch is present in the hypodermal layer. As the endosperm tissue develops, the inner pericarp begins to collapse, leaving only the narrow inner epidermis. The latter forms a thin hyaline layer and is pushed against the surviving cell layers of the outer pericarp (Pl. III, Fig. 35). In the mature grain this structure appears as a thin, whitish coat around the nutlike caryopsis, but it is not fused with the testa. Some of its cells are empty, and others may contain starch grains (Fig. 36). This covering is peeled off in threshing.

Discussion

The systematic position of the genus Eleusine, which is generally placed under the tribe Chlorideae, is not fixed. Hubbard (12) assigns it to the Eragrosteae, whereas Hitchcock (11) includes it under the Festuceae. It would therefore be worth while to compare its embryology with that of other members of these tribes in order to adduce differences among the various genera.

The campylotropous ovule is invested with two integuments. Krishnaswamy and Ayyangar (16) report that the outer integument may take part in the formation of the micropyle. However, this condition was not observed in the present investigation.

Megasporogenesis is normal and results in the formation of a linear tetrad of spores. Stover (31) describes the occurrence of T-shaped tetrads in Eragrostis, a member of the Eragrosteae, to which tribe the genus Eleusine has also been assigned. The embryo sac conforms to the monosporic Normal type reported for other grasses. The synergids are ephemeral, degenerating before the entry of the pollen tube. Variations occur in the structure and

behavior of the antipodals. The primary antipodal cells do not divide, but remain uninucleate, as in *Eleusine indica* (8). In rare cases, however, four or even five cells are present. This is in contrast to the large number of aggressive antipodals observed in other millets, such as *Paspalum scrobiculatum* (23) and *Pennisetum typhoideum* (21), which belong to the tribe Paniceae. Swamy (32) reports a similar feature in Eragrostis, and Shadowsky (29) does so for Cynodon, a genus of the tribe Chlorideae.

The genus Eleusine agrees with Eragrostis in the occurrence of uninucleate antipodal cells, in their lateral displacement before final obliteration, and in the presence of an epiblast. In both, the inner integument takes part in the formation of the seed coat. The inclusion of Eleusine under the Eragrosteae instead of the Chlorideae, therefore, appears to be justified. In Chloris and Seslaria (29) of the Chlorideae, although there is a small number of antipodals, these are multinucleate and retain their chalazal position, thus differing from Eleusine. Eleusine agrees, however, with Cynodon in the lateral displacement of the antipodals.

Fertilization and embryogenesis follow the usual course described for grasses in general. The presence of rudimentary stomata in the epidermal layer of the coleoptile lends support to the view that it may be a modified leaf, although a careful search failed to locate any bud in its axil, such as has been recorded in Hordeum (14).

The endosperm is of the Nuclear type characteristic of the Gramineae. The aleurone layer is usually not more than one cell thick, but it may appear double-layered in certain regions, as it does in Oryza (13) and Poa (2).

As Randolph (28) rightly observes, there is a conspicuous lack of uniformity in the use of the term "seed coat" when applied to the grass seed. Workers have used it to denote the various structures that go to make up the tough protective covering around the kernel, but in a scientific sense it applies only to the inner integument which forms the persistent tegmen. In order to avoid confusion, the various structures that form the protective covering for the mature seed—such as the pericarp, the inner integument, and the nucellar epidermis—have been referred to separately in the present paper. Unfortunately, there is no clear and precise reference in the literature to the persistence or disappearance of these structures in the mature grain. Our existing knowledge of the subject has accordingly been summarized in Table I.

TABLE I

A Summary of Research to Date on the Structure of the Seed Coats of the Mature Caryopsis in Different Tribes of Grasses

Tribe and species investigated	Author	Structure of the wall of the mature caryopsis			
		Nucellar epidermis	Inner integument	Pericarp	Aleurone layer
Oryzeae					
Oryza sativa (common rice)	Teradu (1928)*	.....	Inner layer persists in thin, reduced form	.....	.....
	Ishikawa and Shibuya (1930)*	.....	Persists but later degenerates into a thin layer	.....	.....
	Santos (1933)*	Perisperm cells tangentially elongated and persistent	.....	.....	.....
O. sativa inapostol	Juliano and Aldama (13)	Thick outer tangential wall present as perisperm	Inner layer persists but loses its identity in being pressed down	All cells greatly stretched and collapsed; compressed walls of outer and inner epidermis remain	1–5
Hordeae					
Triticum monococcum, T. dicoccum, and hard wheats	Alexandrova (1)	.....	.....	Only the two epidermal layers persist; mesocarp absent; 5–6 layers persist in hard wheat	3–4
Hordeum vulgare	Haberlandt (9)	.....	.....	.....	3–4
Chlorideae					
Eragrostis cilianencis	Stover (31)	A definite layer present	Both outer and inner layers present	.....	.....
Eleusine coracana	Narayanaswami (present work)	Absent	(Same as above)	Outer pericarp and narrow epidermal layer persist	1 (rarely 2)

Spartina townsendii	Van Schreven (33)	No sharp delimitation	Thick cuticularized outer wall of inner integument persists except at the side of the funicle	5–8 cell layers present, firmly compressed	.....
FESTUCEAE					
Poa pratensis, P. compressa	Andersen (2)	A definite and distinct row present	Suberized layers of outer and inner integuments tightly compressed	Ovary-wall cells compressed into a thin layer	1 or 2
MAYDEAE					
Zea mays	Randolph (28)	Nucellar membrane present	Well-defined layer lacking; occasional scattered noncellular remnants present as a discontinuous layer	Outer and inner pericarp persist; middle regions collapse	.....
Euchlaena mexicana	Cooper (7)	Nucellar epidermis present	.....	.....	.....
ANDROPOGONEAE					
Saccharum officinarum	Artschwager, Brandes, and Starrett (3)	.....	Inner layer persists	Outer and inner epidermal layers, only, present	.....
Sorghum vulgare	Artschwager and McGuire (4)	.....	(Same as above)	All cell layers retained	.....
S. durra	Narayanaswami (unpublished data)	Nucellar membrane present	Inner layer obliterated in certain regions	Only middle layers collapse	1
PANICEAE					
Pennisetum typhoideum	Narayanaswami (21)	Suberized nucellar membrane, only, present	Completely obliterated	All cell layers retained	1 (rarely 2)
Setaria italica	Narayanaswami (22)	A definite layer, with outer tangential wall suberized, present	Rim, only, survives	Outer and inner epidermal layers, only, retained	1
Paspalum scrobiculatum	Narayanaswami (23)	Suberized nucellar membrane, only, present	(Same as above)	All cell layers retained	1 (rarely 2)
Panicum miliare	Narayanaswami (24)	A definite layer present but cells collapsed	Completely degenerates except for rim	Outer and inner epidermal layers retained	1
P. miliaceum	Narayanaswami (24)	(Same as above)	(Same as above)	Occasionally all layers retained	1
Echinochloa frumentacea	Narayanaswami (25)	Occasionally a definite layer present	Rim survives	Outer and inner epidermal layers retained	1

*Cited by Juliano and Aldama (13).

In the genus Eleusine, both cell layers of the inner integument survive to form the tegmen, as they are also reported to do in Eragrostis (31). The cells show brown deposits, probably of tannin, similar to those in Johnson grass seed (10). Early resorption of the entire nucellus leaves no trace of nucellar tissue. The pericarp does not fuse with the inner integument, and the fruit, in spite of the title of this paper, is not a true caryopsis. Until more work has been completed on the seed development of other members of the various tribes it will not be possible to discuss the systematic position or the affinities of the genus in greater detail.

Summary

In this paper the floral structure of *Eleusine coracana* has been described. The embryogeny of the plant and the distribution of its vascular supply have been traced in detail, and the structure of the mature embryo has been studied in both longitudinal and cross sections. The findings may be summarized as follows:

1. The ovules are bitegminal, campylotropous, and tenuinucellar. Meiosis is normal, and embryo-sac formation conforms to the Polygonum type. The three primary antipodal cells usually do not divide, and they remain uninucleate. They are laterally displaced during the development of the endosperm, before final resorption.

2. Occasionally the antipodals simulate an egg apparatus. The synergids are ephemeral.

3. Syngamy and triple fusion occur simultaneously.

4. The endosperm development follows the conventional pattern. Frequently a double layer of aleurone is observed. Involution of the aleurone also occurs.

5. The nucellar tissue, including the nucellar epidermis, is completely obliterated. The inner integument (tegmen) persists to form a true seed coat. The layers comprising the inner regions of the pericarp collapse; only the outer pericarp, consisting of the outer epidermis and a few underlying layers, together with the inner epidermis, survives.

6. The pericarp is never fused with the inner integument. The grain is, therefore, not a true caryopsis.

Acknowledgment

I am grateful to Professor P. Maheshwari, University of Delhi, India, for his guidance and encouragement.

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University of Michigan

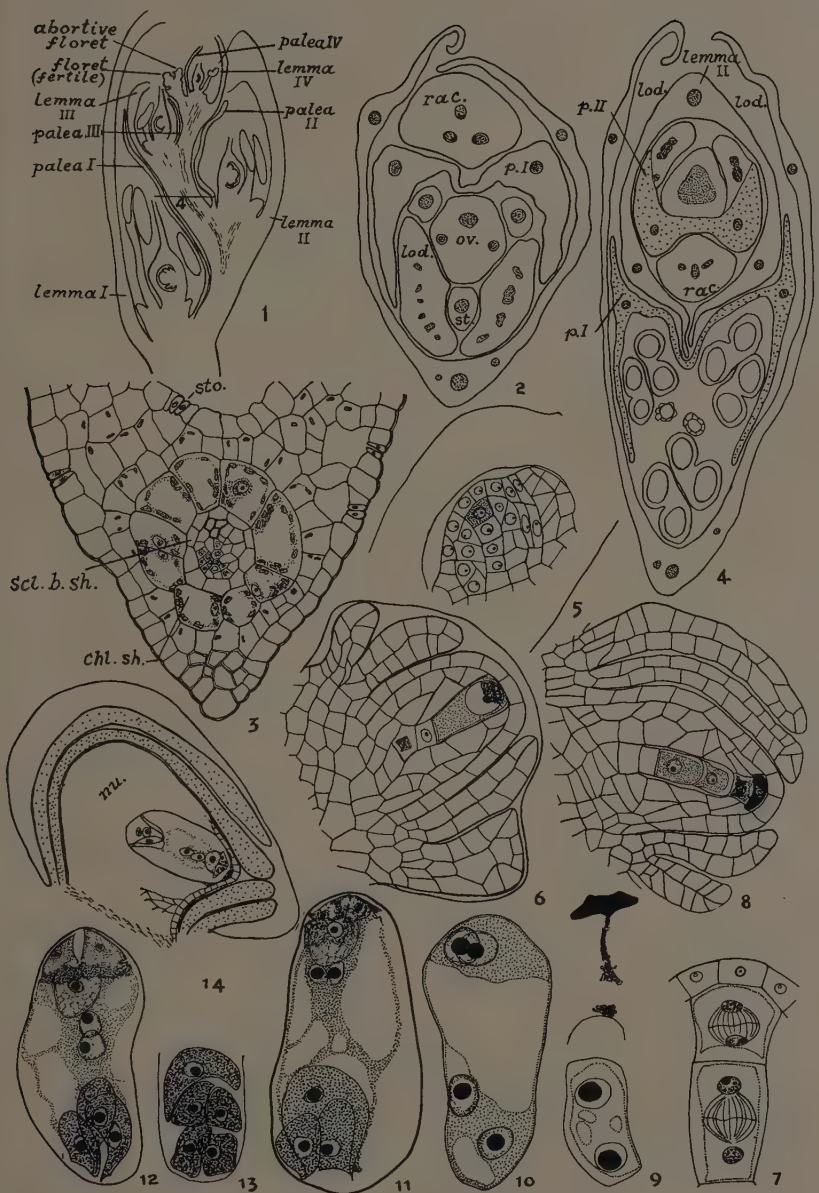
PLATES I–III

EXPLANATION OF PLATE I

Eleusine coracana—structure of spikelet and embryo sac formation

FIG. 1. Longitudinal section of spikelet with lower empty glumes removed. × 100
FIG. 2. Cross section of spikelet through first floret. × 100
FIG. 3. Cross section of lemma I through midrib. × 226
FIG. 4. Cross section of spikelet through base of second floret. × 100
FIG. 5. Young ovule, showing archesporial cell mounted on an axial row of nucellar cells. × 226
FIG. 6. Ovule, showing enlarged megaspore mother cell. × 226
FIG. 7. Second meiotic division in dyad cells. × 440
FIG. 8. Ovule, showing linear tetrad of megaspores. × 226
FIG. 9. Binucleate embryo sac. × 440
FIG. 10. Four-nucleate embryo sac. × 440
FIGS. 11–12. Organized embryo sacs. × 226
FIG. 13. Antipodal complex of five uninucleate cells. × 226
FIG. 14. Longitudinal section of ovule, showing campylotropous condition. × 100

ABBREVIATIONS: *chl. sh.*, chlorophyllose sheath; *lod.*, lodicules; *nu.*, nucellus; *ov.*, ovary; *p.*, palea; *rac.*, rachilla; *scl. b. sh.*, sclerenchymatous bundle sheath; *st.*, stamens; *sto.*, stomata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floret (fertile)
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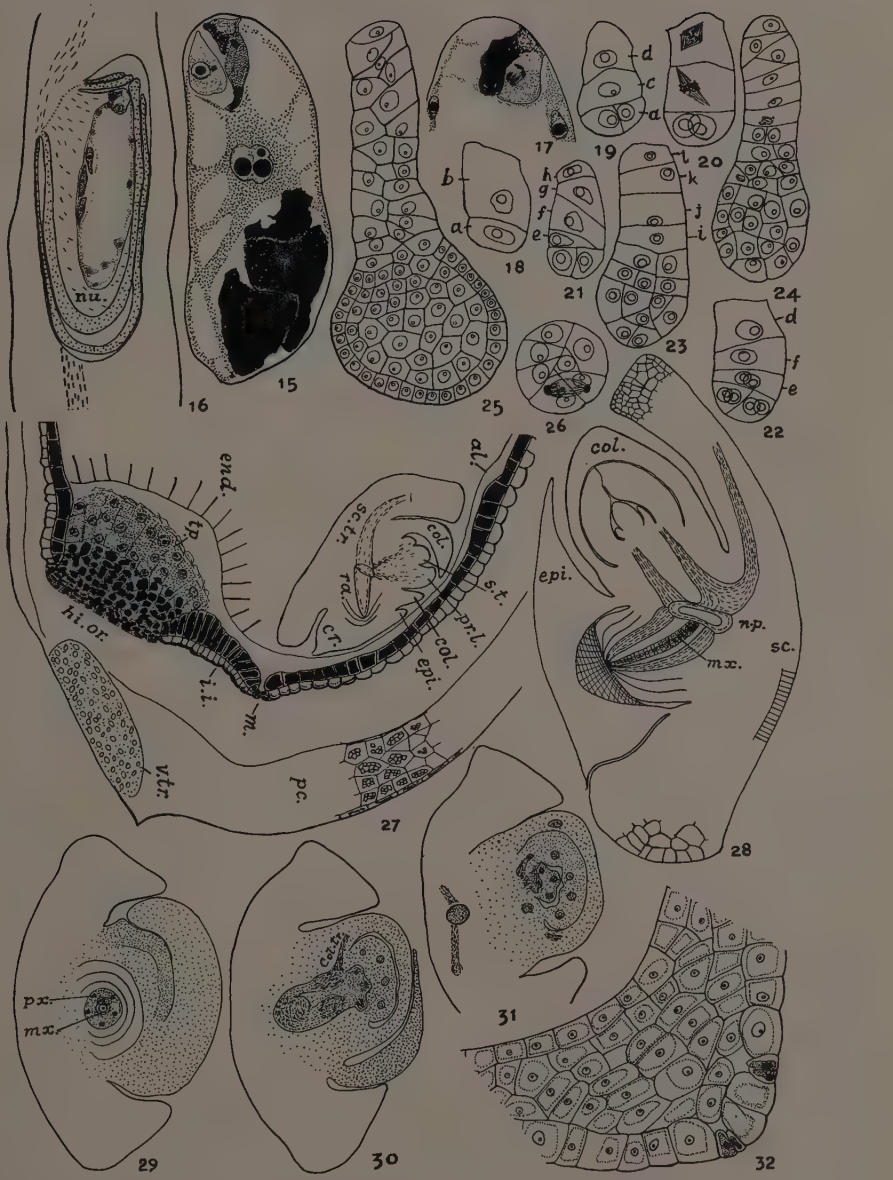
EXPLANATION OF PLATE II

Eleusine coracana—development and structure of embryo

FIG. 15. Syngamy and triple fusion. × 226
FIG. 16. Ovule, showing zygote surrounded by endosperm nuclei. × 42
FIG. 17. Anaphase in zygote. × 226
FIG. 18. Two-celled proembryo. × 226
FIG. 19. Four-celled proembryo. × 226
FIG. 20. Proembryo, showing division in basal cells. × 226
FIGS. 21–25. The proembryo at different stages of development. × 226
FIG. 26. Cross section of proembryo at about the stage shown in Figure 23. × 226
FIG. 27. Longitudinal section through lower part of grain. × 42
FIG. 28. Longitudinal section of mature embryo. × 48
FIGS. 29–31. Series of cross sections of mature embryo. × 48
FIG. 32. Longitudinal section of apex of coleoptile. × 226

ABBREVIATIONS: *al.*, aleurone layer; *col.*, coleoptile; *col. tr.*, coleoptile trace; *cr.*, coleorhiza; *end.*, endosperm; *epi.*, epiblast; *hi. or.*, hilar orifice; *i.i.*, inner integument; *m.*, micropyle; *mx.*, metaxylem; *n.p.*, nodal plate; *nu.*, nucellus; *pc.*, pericarp; *pr. l.*, primary leaf; *px.*, protoxylem; *ra.*, radicle; *s.t.*, stem tip; *sc.*, scutellum; *sc. tr.*, scutellum trace; *tp.*, tapetum; *v. tr.*, vascular trace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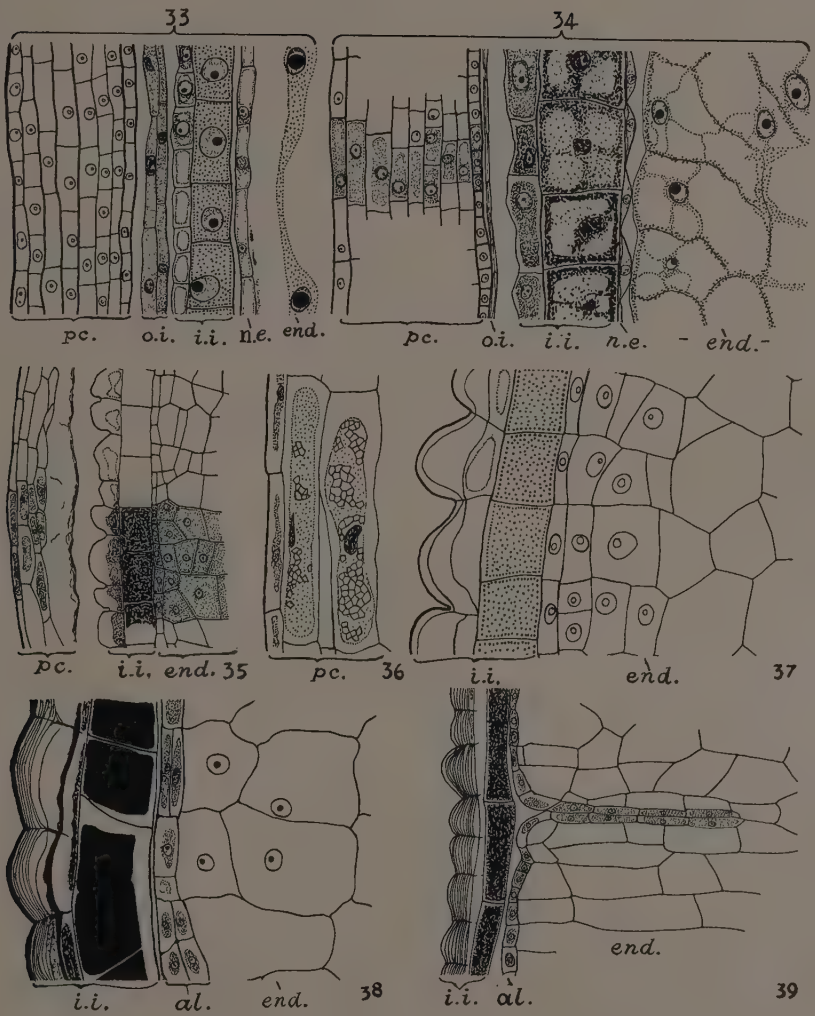
EXPLANATION OF PLATE III

Eleusine coracana—structure of endosperm and seed coat

FIG. 33. Peripheral portion of caryopsis at free nuclear stage of endosperm. × 240
FIG. 34. Caryopsis wall at cellular phase of endosperm. × 240
FIG. 35. Caryopsis wall, later stage. × 106
FIG. 36. Outer portion of pericarp. × 240
FIG. 37. Inner integument and radial rows of endosperm. × 240
FIG. 38. Inner integument and endosperm, later stage. × 240
FIG. 39. Peripheral portion of mature kernel, showing involution of aleurone. × 106

ABBREVIATIONS: *al.*, aleurone layer; *end.*, endosperm; *i.i.*, inner integument; *n.e.*, nucellar epidermis; *o.i.*, outer integument; *pc.*, pericarp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THE GENUS LYSURUS

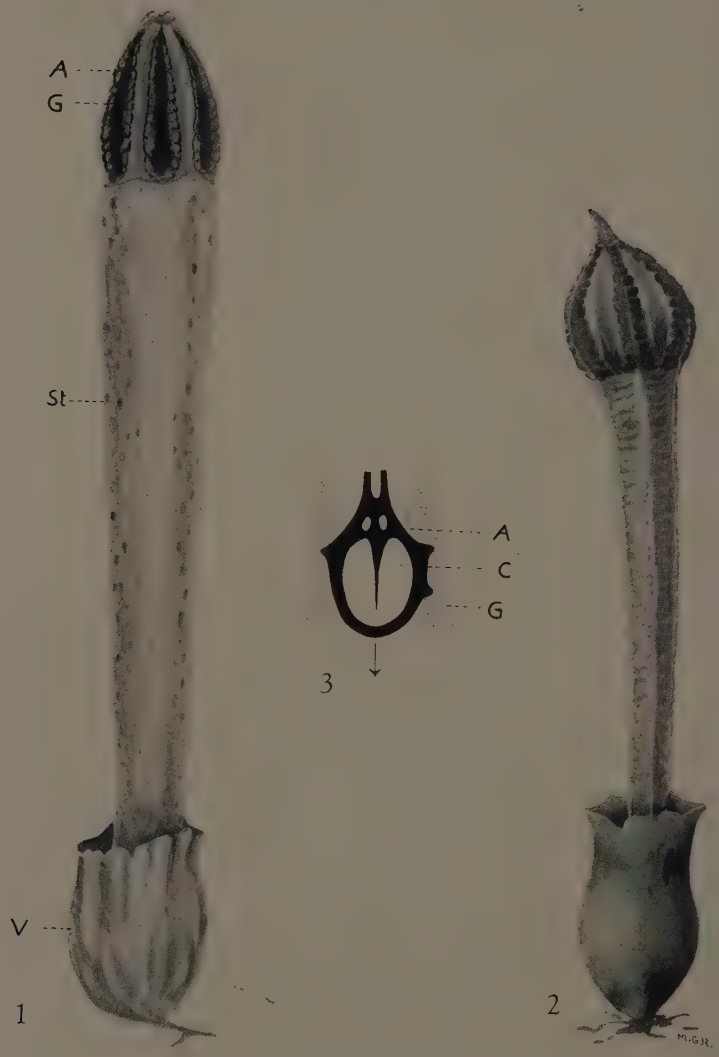
PAUL M. REA (AND BERTA HEIDENHAIN)*

THE genus Lysurus was established by Fries in 1822 on *L. mokusin*. In the following years many somewhat similar fungi were discovered; some of them were assigned to Lysurus, and others were placed in the closely related genus Anthurus. Most of the early information, however, was incomplete, and considerable confusion developed in regard to both genera. The treatments by Cunningham (1942), Fischer (1933), and Zeller (1948) illustrate this confusion.

Attention was again drawn to this situation when collections of *Lysurus mokusin* and *Anthurus borealis* were made in Santa Barbara, California. Only a few specimens of *A. borealis* were found, but *L. mokusin* was discovered in great abundance, more than four hundred specimens being collected. Such a wealth of material in the fresh state had certainly never been available for study before. It is not surprising, therefore, that this material, covering the whole life history of the fungus, discloses information that changes profoundly the current concepts of the morphology and the development of the species. Moreover, it affords a basis for clarifying the distinctions between the two genera.

The present paper, then, focuses attention on two points: the taxonomy of the genus Lysurus and a theory about the morphological relationship possibly existing between the Clathraceae and the Phallaceae.

* Paul Marshall Rea died in 1948, before he had published this investigation. The preliminary drafts of his paper and the specimens of *Lysurus mokusin* were given to the University of Michigan by Mrs. Rea. Professor Alexander H. Smith asked me to prepare the manuscript for publication. As presented, the paper is almost completely taken from the main drafts by Mr. Rea. Three paragraphs have been added by me—the introduction, the description of the development of *Anthurus borealis*, and the discussion of the relationship of the Clathraceae to the Phallaceae.—Berta Heidenhain, Delaware State College, Dover, Delaware.



FIGS. 1–3. *Anthurus borealis* (Fig. 1) and *Lysurus mokusin* (Figs. 2–3)

(See explanation on facing page.)

The Taxonomy of the Genus Lysurus

Anthurus borealis Burt, 1894

(Fig. 1)

Anthurus borealis is treated here for purposes of comparison with *Lysurus mokusin*. It has been reported many times from Massachusetts, Connecticut, New York, Ohio, and Washington, D.C., and is now recorded from Santa Barbara, California.

Morphology.—Total height 10 cm.; volval cup 3 cm. high, 1.5–2.5 cm. wide; stipe about 8.5 cm. long, 12 mm. thick above, tapering to 9 mm. at top of volval cup, terete, white, tinted above with brownish yellow, hollow, the central cavity 4–4.5 mm. wide, the wall 3.5–4 mm. thick, containing an inner ring of large vesicles that intercommunicate to form about thirteen longitudinal tubes, which show externally as a faint but distinct longitudinal striation, and an outer irregular ring of smaller, more numerous vesicles, some of which are externally perforate; stipe divided above into five erect arms each slightly separated from the next except at their tips, which, when specimen was first collected, were united but outlined by definite seams and which later separated, and externally bearing a median, longitudinal, pale-orange ridge surmounted by a groove which is narrow in its middle portion but broader and shallower below and which disappears at the very slight groove that separates the arms from the stipe as well as at the apex of the arms. Inner and lateral surfaces of the arms bearing irregular, predominantly transverse wrinkles, knobs, and similar outgrowths, a transverse section in the middle of the arms showing one large tubular cavity and two smaller cavities, one on either side of the dorsal groove.[1]

[1] I am not able to show a picture of this transverse section, since I could not find one among Rea's drawings. There are two illustrations in the literature, a photograph by Lloyd and a drawing by Burt. Both of these illustrations, however, are slightly different from Rea's description, since they show the arms of Anthurus as

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EXPLANATION OF FIGURES 1–3

Fig. 1. *Anthurus borealis*, fully developed fruiting body showing volva (*V*), stipe (*St*), and the arms of the receptacle (*A*), which bears the gleba (*G*). (After Burt.)

Figs. 2–3. *Lysurus mokusin*, fully developed fruiting body (Fig. 2) and cross section of an arm of the receptacle (Fig. 3). The arm (*A*) includes one main cavity (*C*) and two smaller cavities. The gleba (*G*) is attached to the lateral sides of the arm. The arrow indicates the direction of the center of the carpophore.

Gleba nearly black, attached to the roughened inner faces of the arms except near their bases and protruding between them, the protruding lobes before deliquescence marked by median vertical grooves (which are not characteristic of *Lysurus mokusin*).

As to the gleba, its base forms a dome above the central cavity of the stipe because on this level the gleba descends farther between the arms than it does on their upper part. To this dome vestiges of the axial gel adhered in our specimens, but there was no transverse, perforated membrane at the level of the base of the dome such as Burt observed and made one of the principal differences between his species and *Anthurus australiensis*. I am convinced that this membrane was merely a remnant of the gel, like that which occurs occasionally in *Lysurus mokusin* as a varnish-like film across the cavity of the stipe or between the arms.

The radial plates are, in the lower part of the volva, attached to the stipe in broad, thin sheets which appeared to be continuous from one plate to another; this accounts for the terete form of the stem without grooved angles. In the upper 1 cm. of the volva, where the plates were attached before expansion to the dorsal ridges of the arms, they were still present as radiating plates; but it was not possible to determine whether they originally stopped short of the apex of the egg, as Burt says they did.

Development.—The development of *Anthurus borealis* has been observed by Burt (1894) and by N. H. White (1944), who described the fungus under its synonym *Lysurus sulcatus*. The following description summarizes the results of both investigations.

The young eggs are first observed as small white swellings on the rhizomorphal strand. A longitudinal section of this stage in Figure 4 shows the tissue as already differentiated in a cortex of loose hyphae surrounding a complex of more densely interwoven central hyphae.[2]

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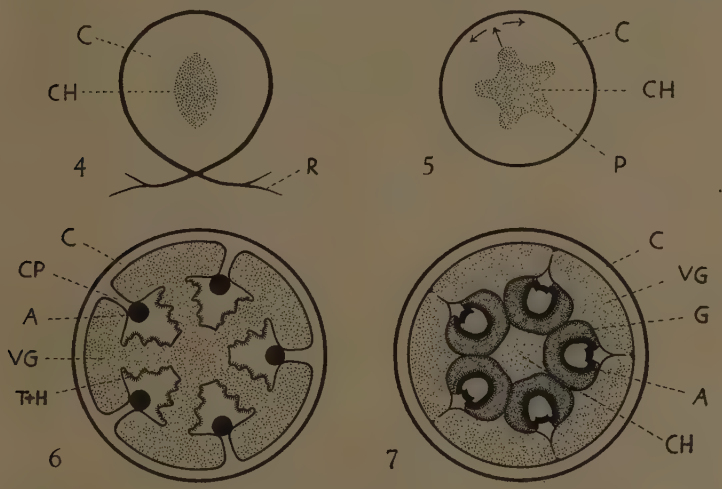
having only one main cavity and no additional small ones. I am convinced that this difference is not important, and that it is probably caused by differences in the plants' habitats.—B. H.

[2] White's illustration of this stage of development shows the central hyphae of the egg as separated from the rhizomorph by the cortex. This figure is certainly not correct because, as Burt writes, the central hyphae of the egg derive from the central hyphae of the rhizomorphal strand and thus form a direct continuation of the rhizomorph's central tissue. White's fungus, I presume, was not different from Burt's specimen; but his longitudinal section was not made exactly through the center of the egg.

Later on, the stipe originates from the lower part of this central complex; more important for our purposes is the development of its upper part. It is from this part that from 4 to 7 longitudinal, fold-shaped prolifications arise which in cross section appear as small protuberances of the central tissue (Fig. 5). These protuberances



FIGS. 4–7. *Anthurus borealis*, schematic drawings of development: longitudinal section of a young egg (Fig. 4); cross sections through eggs in older stages (Figs. 5–7). Abbreviations: *A*, arm of the receptacle; *C*, cortex; *CH*, central hyphae; *CP*, cortical plate; *G*, gleba; *P*, protuberance of the central hyphae; *R*, rhizomorph; *T* + *H*, trama and hymenium; *VG*, volva-gel. The arrows in Figure 5 indicate the direction in which the protuberances of the central hyphae grow. (Figs. 4–5 after White's description; Figs. 6–7 after Burt.)

grow centrifugally, and their tops thicken and broaden laterally, a way of growing that has two results which are shown in the next stage (Fig. 6). First, the tops of the protuberances form a thick layer of hyphae adjacent to the cortex. This layer is called "volva-gel," because the hyphae undergo a gelatinization. Secondly, the growing protuberances compress the cortical tissue in the peripheral region of the egg as well as between their own lateral edges. The compressed tissue between the edges forms longitudinal plates, which

are called "cortical plates." From the inner margin of these plates the arms of the receptacle later develop. The gleba differentiates in the following way: On the narrow base of each branch of volva-gel small outgrowths arise. These outgrowths are the beginning of the trama. Later on they become larger and richly branched and are finally covered with the hymenium. Trama and hymenium, together constituting the gleba, grow and fill, finally, the space between the volva-gel branches and the arms of the receptacle. As a cross section of a very advanced stage shows (Fig. 7), the gleba comes into contact with the arms and covers their inner and lateral sides. Only the dorsal groove of the arms remains free of it.

At maturity the central hyphae, the tissue of the volva-gel, and the tissue of the cortical plates dissolve. The carpophore which bears the receptacle and the gleba on its top elongates and ruptures the apex of the volva.

Lysurus mokusin (L.) Fries, 1822

Distribution.—This species was first described in 1774 by Rev. P. Cibot, a missionary in Peking, as "Mo-ku-sin"; his paper and illustrations are remarkable for their scope and accuracy. If the relatives of the species had been equally well described by subsequent authors, our taxonomic difficulties would be few. The fungus has since been reported from China, Japan, and Australia as *Mutinus pentagonus* Bailey, 1895 (see Lloyd, 1907). In the United States, six plants were collected in 1907 near a rotten haystack at Denton, Texas, by Long, who reported them in 1917, referring the fungus doubtfully and provisionally to *Lysurus texensis* Ellis, a nomen nudum. In 1916 and in at least one season thereafter it was collected in a greenhouse in Chicago, California, by David Griffiths and communicated by L. C. Krieger to Lloyd (1916–19), who reported it. Mr. I. A. Stevenson informs me in a letter that in a number of seasons since 1919 it has been found near the Smithsonian Institution and the Treasury Department building and in other localities in Washington, D.C. Miss Templeton collected several specimens in Los Angeles in 1946.

In Santa Barbara, *Lysurus mokusin* was first collected in the garden of Miss Caroline Hazard, in November and December 1936 (four plants); then in the gardens and lawns of Miss Emma Murphy (three plants in 1941), Miss Kate Walker (sixty-six in 1943–46), Mr. W. L. Beckwith (twenty-five in 1944–45), Mr. Kenneth Tisdell

(eight in 1945), and Mrs. John R. Sackrider (four hundred in 1944–47). Thanks are due all of these, especially Mrs. Sackrider and her daughter Miss Harriet Sackrider, who for more than four years faithfully inspected their lawn daily and reported each fruiting body. Fortunately, they were only six blocks away from the laboratory, so that collections could be made promptly. It is unlikely that they missed many specimens, although not all the withered ones were picked. About 75 per cent of those collected had expanded or hatched from mature eggs, which means a higher proportion of perfect specimens. The rest have been studied as eggs, in all stages from 1 mm. in diameter to full size.

Habits.—The habits of the plant cannot be better described than in the words of Cibot: "It usually completes its expansion within a space of twelve hours and when complete begins immediately to become limp, bent, sinks down and undergoes putrefaction; yet this rarely happens to it because various insects, most greedy for this substance, usually besiege the fungus as it emerges from the ground and consume almost all of it before it attains a perfect stage of growth." Cibot thought it especially associated with the mulberry, and with humid places in warm weather. In Santa Barbara it grows in dry, hard ground as well as in abundantly watered gardens and lawns. Indeed, the largest fruiting bodies, over 12 cm. tall, grew in hard ground and from very large eggs, as is shown by the size of the volval cup. This is probably because such eggs have to develop for a long time and to a large size before they accumulate the power to break through the surface. These specimens tend to carry up a part of the apex of the volva as a calyptra. In soft, well-watered ground, however, smaller eggs are able to push through the surface, and produce plants of medium and small size.

The seasonal distribution of the fungus is remarkable. Fruiting occurs every month of the year in Santa Barbara, with the height of the season at different times in different years. Generally, the months from May to October have been the most prolific, but in 1946 the Sackriders found no specimens from July to September; fruiting began that year in October and continued through the winter, with an increased number of plants in March and April(?), which had previously been a lean period.

The time required for the complete expansion of the fruiting body was studied on November 7, 1944. At 3:30 P.M. a fine, large

specimen 15.2 cm. tall, fully expanded and arched over, was collected about two feet from where two others had been collected at 11:30 A.M. and where the ground had been searched carefully for signs of eggs. It is certain that the afternoon specimen had developed during the four-hour interval.

Morphology.—Fries described Lysurus as having free arms, and based the name (from *lusis* 'loosing' and *oura* 'tail') on this trait. The Santa Barbara material, however, shows that the arms are free only when broken, and that normally they are united apically and surmounted by a resumption of the stem structure. The form of the expanded plant (Fig. 2) may therefore be likened to a moat (the volval cup) surrounding the base of a tower (the polygonal stipe) bearing a belfry or lantern (the receptacle) surmounted by a spire. The gleba is equally distinctive, consisting of a series of segments originating outside the lantern, one in each of the peripheral gel chambers, and inserted in the vertical slits between the arms or pillars of the lantern, but not invading its central chamber. *L. mokusin* thus differs in a very important way from Burt's species and from all other members of the Clathraceae.

The Santa Barbara specimens range in total height from 3 to 16.5 cm., depending on the conditions of growth. The mode is 7.5 cm.; the median and average are both 8.8 cm. Eight of our specimens were 12 cm. tall; four, 13 cm.; two, 14 cm.; and one, 16.5 cm.

In the following paragraphs each part of the fruiting body of *Lysurus mokusin* will be described in detail.

The *eggs* develop a few centimeters below the surface; when ready to dehisce they have attained a height of 2–6 cm., with the tops usually just showing above ground. They are strongly gregarious to caespitose, sometimes occurring in a cluster of a dozen or more, with the eggs varying from 1 mm. in length to full size. They are white and have at the base one or many rhizomes. Their size is only an approximate indication of the stage of development. Dehiscence is by radial fissures at the top.

The *volval cup* ends in more-or-less triangular lobes above. It is lined inside by the yellowish, varnish-like, dried gel, with interruptions by the white radial plates, which, after tearing loose from the sporocarp during expansion, collapse in pleats on the volval wall.

The *stipe*, when fully expanded, is up to 13 cm. long and 2.5 cm. in diameter at the top, tapering downward to a point only about 2

mm. thick at the base and resting loosely in the bottom of the volval cup; it varies from flesh pink to bright pink above, and pales gradually to white at the base. Plants not fully expanded have the stipe more nearly equal in diameter above the rim of the volva. Externally the stipe has the form of a polygonal prism with from four to seven strongly salient angles. About 16 per cent have four angles; 75 per cent, five; and 9 per cent, six; seven angles have been observed in only two specimens. The number of angles on the stipe corresponds to the number of arms or pillars in the lantern above, the number of angles in the apical spire, and the number of the radial plates. Each angle is surmounted by a groove, up to 3 mm. wide, with fimbriated edges where the radial plates were attached before dehiscence. The surfaces between the angles vary from slightly concave to deeply V-shaped and have a slightly blistered appearance due to the vesicular structure of the stipe, but the blisters are not ordinarily perforated unless they have been damaged by insects or, sometimes, perforated in drying.

The stipe is tubular, and its cavity may contain irregular strands or films of varnish-like dried gel. The wall contains about fourteen longitudinal tubes with few if any septa, the tubes being polygonal in section and having paper-thin walls. In the angles there are in addition about three smaller tubes in triangular arrangement, the outermost one forming the groove on the angle when the radial plate is torn loose. The stipe thus consists of a series of triangular prisms, each of them containing about five tubes. The prisms form the angles of the stipe, having very thin connections with one another. This explains why, when expansion is complete, V-shaped depressions alternate with the salient angles of the stipe.

The *arms* or pillars of the lantern are direct continuations of the prisms that form the angles of the stem. They alternate with vertical slits in line with the V-shaped depressions in the sides of the stipe. It is appropriate, therefore, to describe the lantern as formed (1) by the failure of the prisms to unite laterally with one another, and (2) by differentiation of the prisms for the function of gleba-bearing; or, since the fertile structure is primary, to describe the stipe as formed by lateral fusions of infertile portions of the arms. The arms are of a deeper color than the stipe, nearly blood red, and range in length from 7 mm. to 40 mm. The median is 16.5 mm., the average 17 mm., and the mode 20.5 mm. As already stated, the

number of arms corresponds to the number of angles on the stipe and varies from four to seven, about 16 per cent of the specimens having four arms; 75 per cent, five; 9 per cent, six; and less than 1 per cent, seven. In cross section (Fig. 3) the arms are subtriangular, with the apex outward and bearing a continuation of the ridge and groove of the stipe angles. The base of the triangle, or inner surface of the arms, is smooth and sterile and faces the central chamber, which is empty after expansion except for occasional strands and films of dried gel. This chamber is directly continuous with the central chamber of the stipe. The five tubes that the arms have before dehiscence persist more or less. The outermost forms the groove in the dorsal ridge when the radial plate is torn loose. The two large, inner ones usually partly fuse, and the remaining two may be present or absent. The sides of the arms, facing laterally and outward, are complexly roughened. The wall itself is slightly folded on the outside, the folds being developed into sinuous ridges which are predominantly transverse and bear plugs and knobs that are more or less elaborate in different specimens. This roughening nearly meets that of the adjacent arm in the crotch.

The arms are usually vertical and very slightly separated one from another, but sometimes they are strongly bowed outward, thus emphasizing the lantern effect. As has been said, they are normally united apically, but when broken may be free and more or less divergent.

The *gleba*, as already noted, consists of wedge-shaped segments fitted into the triangular spaces between adjacent arms and attached to their roughened sides, but not invading the central chamber of the lantern. It is usually light brown when first exposed, becomes dark brown during deliquescence, and finally dries almost black. White tramal strands run through the gleba before deliquescence and in longitudinal sections are clearly evident radiating from the rough surface of the arm. There is no median vertical groove or seam until the gleba sinks along this line in deliquescence. The chambering of the gleba appears to have no unusual features. Spores are produced in enormous quantities and are nearly hyaline under the microscope: they are cylindric-elliptic, 3.6–4.2 × 1.5–1.8 μ.

As for the *spire*, this extraordinary structure is formed by the apical union of the arms and shows all features of resumption of the stipe formation in miniature: color, polygonal cross section with

salient angles bearing continuations of the groove to which the radial plates are attached, minute tubular vacuolization, and continuation of the central chamber to the tip, where it is closed. The spire is more or less tapering, being as much as 5 mm. thick at the base; it may be erect or, especially when it is very long, bent down beside the arms. The length of the spire varies from 1 mm. to 23 mm., the average being 5 mm. and the mode being 3.5 mm. The best development of such a structure is seen in *Staheliomyces cinctus* Ed. Fischer (1921 and 1923), of the Phallaceae; there it suggests interesting morphological possibilities that will be discussed in the final section of this paper.

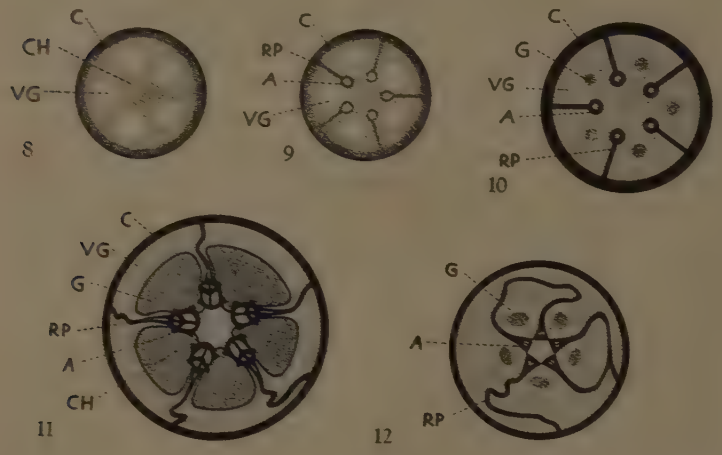
Development.—The white mycelial cords or rhizomorphs from which the egg develops consist of a core of loosely interwoven hyphae that are 2–6 μ thick, sinuous, or straight for considerable distances, branching, septate, and often with clamp connections up to 10 μ thick, and a cortex of more densely interwoven hyphae that are up to 12 μ thick, sinuous, branching, septate, with many clamp connections, and more or less densely encrusted and interspersed with calcium-oxalate crystals.

The egg is a simple, globular, then ovate, enlargement of the mycelial cord, in which the core forms the uniform, undifferentiated ground tissue and the cortex forms the cortex of the egg, or the volva. Since eggs vary greatly in size at maturity, it is impracticable to correlate the stages of development with egg diameters, but these will be mentioned as general indications.

The first differentiation, seen in cross section of an egg about 1 mm. in diameter, is gelatinization of the ground tissue in five small areas halfway between the center and the cortex. These clear spots are the beginning of the peripheral gel and give the section the appearance of a wheel with a solid hub and very thick spokes (Fig. 8). At an only slightly more advanced stage (Fig. 9) the following developments are seen: the peripheral gel chambers are larger. The central line in each spoke shows a denser arrangement of the ground-tissue hyphae, the beginning of a radial plate. Where each plate joins the hub a minute area of gelatinization marks the beginning of the first cavity of the arm, and around it the ground tissue forms a slightly denser ring. At the center of the hub and between the arms gelatinization is beginning, thus establishing the axial chamber of the sporocarp, often called the columella, and fore-

casting its communication, through the slits between the arms, with the peripheral gel. In all this gel tissue the hyphae become more loosely arranged, but retain their ability to form complex new tissues, as will be shown.

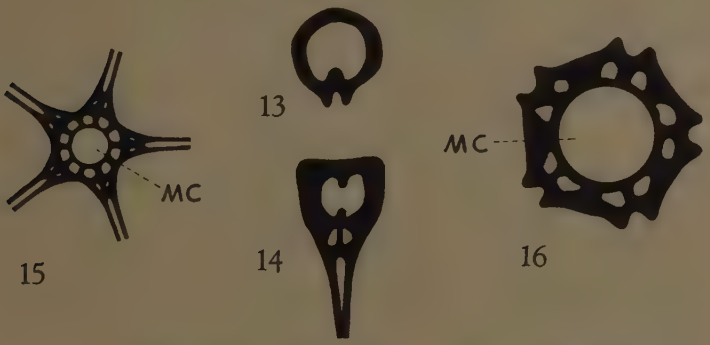
When the egg has reached a diameter of about 2 mm. the differentiation described above is well advanced. Cross sections (Fig. 10) show the radial plates as thin, dense, white tissues extending



FIGS. 8–12. *Lysurus rubrisin*, cross sections of eggs in various stages of development. Abbreviations: *RP*, radial plate; other letters as in Figures 4–7. The cross section in Figure 12 shows the ability of the radial plates to lose contact with the cortex and to anastomose with one another.

from the cortex to near the center of the egg, where they end in thin, dense, white, very small rings, which are the arms. Gel tissue is everywhere: in the cavities of the arms and in the axial cavity, or columella, which serves as communication between the arms and the larger peripheral gel chambers. At about this time the first stage of gleba formation may be seen. It appears as a small white spot with fimbriated edges in each peripheral gel chamber, definitely outside the circle of arms and separated from them by a space of at least its own diameter. The white spots result from differentiation and concentration of the gel hyphae to form the beginning of the

trama of the gleba. The fimbriated edges are due to the radial extension of these tramal hyphae into the surrounding clear gel. Because the gel is transparent at this stage, observation of developing structures is much more informative than after it has been coagulated by fixing fluids. The development of the hymenium and the complex glebal chambers appears to be in the usual manner, but has not been especially studied.



FIGS. 13–14. *Lysurus mokusin*, cross sections of two arms of the receptacle. The younger arm, in Figure 13, has developed only one cavity, whereas the older one, in Figure 14, shows the main cavity and three smaller cavities.

FIGS. 15–16. *Lysurus mokusin*, cross sections of the spire (Fig. 15) and the stipe (Fig. 16). The similarity of the two sections shows that the principle of the stem is maintained up to the top of the carpophore. *MC*, main cavity.

All the essential tissues are now differentiated in their earliest stages; the rest of the development is a matter of their elaboration and their increase in size. We shall treat each structure in turn.

As the arms grow larger the hyphae of their walls are gradually transformed into pseudoparenchyma and the number of their tubular cavities increases. The primary tube (Fig. 13) first becomes double, then the septum is partly absorbed and leaves again a single tube, but with two internal ridges, the remnant of the septum. Between this tube and the junction with the radial plate two very small tubes then form, and beyond them a third, which is the inner end of a split in the radial plate near its junction with the arm (Fig. 14). The split may occur very early or quite late in the develop-

ment, but when the plate is finally torn loose in expansion the inner edge of the split forms the characteristic groove in the external ridge of the arm, stem, and spire. By now (Fig. 11), each glebal segment has grown so that it fills the greater part of its peripheral gel chamber, and its inner edge has advanced between two adjacent arms and comes into contact with their roughened surfaces. At this stage the great amount of the glebal mass that lies outside the arms is noteworthy. The gleba is now becoming pale brown and beginning to produce spores, while the pseudoparenchymatous walls of the arms are turning red.

The white radial plates, which at first ran straight to the cortex, soon become sinuous in the area between the glebal segments and the cortex, and at length show a surprising ability to detach themselves from the latter in various places and to form new anastomoses, either with the cortex or with one another. In thick hand-sections of fresh eggs they may often be seen wandering through the volval gel in a complex pattern which varies at different levels (Fig. 12). The peculiar behavior of these plates has an important relation to the development of the sporocarp, but before describing this it will be helpful to consider the structure of the egg as seen in longitudinal sections.

The peripheral gel chambers extend from the base to the apex of the egg, like the segments of an orange. Between them, as vertical partitions, lie the radial plates, which meet toward the apex of the egg and nearly meet at the base; elsewhere their inner edges are at a considerable distance from the vertical axis of the egg. Along the entire, inner, free edge of each plate, the ground tissue is differentiated into a pseudoparenchymatous, triangular prism containing about five vertical tubes, and the radial plate is split where it joins the edge of the prism. In the upper part of the egg the lateral edges of these prisms unite to form the spire (Fig. 15). Through most of the egg below the spire the prisms fail to unite laterally and thus produce the vertical slits that separate the arms. In the lower quarter of the egg the prisms once again join laterally to form the stipe with its thin side walls and thick salient angles (Fig. 16). When the radial plates are finally torn loose in expansion, they leave a continuous vertical groove with fimbriated edges on the outer margin of each prism, from the base of the stipe to the tip of the spire. In the vertical axis the gel fills a continuous tubular cavity, the columella,

which is closed at the base of the stipe and the tip of the spire but communicates with the peripheral chambers through the slits between the arms.

The gleba is precocious in development, and, until the egg is near maturity, its segments fill the greater part of the egg, extending somewhat above and below the arms but attached only to their roughened sides; most of its mass lies in the peripheral gel chambers. With the relatively greater growth of the lantern as dehiscence approaches and with the final elongation during expansion, each glebal segment finally comes to fit neatly into the V-shaped space between two adjacent arms.

So little space is available in the base of the egg for the tall stipe that its wall becomes elaborately plicated, as in stipitate phalloids generally. The apical spire is similarly pleated; it remains upright if its length is only a few millimeters. When it is long, and it must be remembered that in half the specimens it ranges from 5 mm. to 23 mm., quite a different adjustment is made, for the spire bends over and grows downward beside the lantern. Since at first the radial plates, which are attached to the angles of the spire, meet at its apex and immediately join the cortex, the spire would be immovable but for the ability of the plates to migrate. In a drooping spire, therefore, they become detached from the apex of the egg and, with their apparently unlimited power of growth, follow the spire in its wanderings, even to the level of the base of the lantern. In this condition the radial plates form a complex of anastomoses that can hardly be unraveled in dissection. Such long, deflexed spires sometimes show a surprising ability to become erect after dehiscence, but often they remain bent.

Significance of the developmental process.—Owing to the classic work of Fischer (1890), the development of Clathrus has served as a standard of comparison in interpreting the development of other species. Fischer's theory is that the development is strongly dynamic, based upon centrifugal processes and forces proceeding from the columella. The peripheral gel segments are conceived of as outward-growing branches of the columella that push the cortex outward, which in turn drags the cortical plates away from the hymenium forming along their inner edges and thus produces the first glebal chambers.

In contrast to Clathrus, as interpreted by Fischer, the develop-

ment of Lysurus is a more static process, all the tissues and structures being developed *in situ* by differentiation of one primitive ground tissue derived from the core of the rhizome. The peripheral gel segments are not outgrowths of the columella. They originate independently and earlier. They cannot stretch the radial plates by pushing the cortex outward, for the plates have length to spare, as is shown by their plication. The peripheral gel is uninterruptedly continuous with the gel which permeates the pseudoparenchyma and gleba and fills all the cavities of the receptacle. The radial plates are not outgrowths of cortical tissue, but are formed *in situ* by differentiation of the primitive ground tissue. The plates are undoubtedly intimately related to the formation of the pseudoparenchyma of the arms, stem, and spire; and it is possible that their hyphae may be differentiated into this tissue. But the evidence indicates strongly that the pseudoparenchyma is chiefly, if not entirely, differentiated directly from the ground tissue adjacent to the inner edges of the plates. In any event, the inner edges of the plates do seem to have a stimulating influence and to act as a catalyst on pseudoparenchyma formation.

But the most distinctive feature of the development of this species is the quite novel formation of the gleba: its origin in the peripheral gel outside the lantern, without contact with any other tissue until it unites with the roughened surfaces of the arms, and its complete absence from the axial or columella chamber. The Santa Barbara material fully confirms the original diagnosis by Fries as to the external position of the gleba, the observations of Patouillard (1890) on this point, and the conclusion of both that Lysurus is monotypic, so far as is known, and represents an approach to the Phallaceae.

Another difference between Clathrus and Lysurus is noteworthy, namely, the construction of the volva. The members of the Clathraceae are generally said to have a volva of three layers. The outer is the membranous cortex derived from the cortex of the rhizomorph from which the egg develops. The so-called middle layer is thick and gelatinous, is derived from the medullary tissue or core of the rhizome, and is divided into compartments by radial partitions called cortical, peridial, or volval plates. They are conceived of as inward growths of cortical tissue and as participating in the formation of the pseudoparenchyma of the receptacle. Strange to say, the inner

layer of the volva is neither described nor figured in any literature I have seen, except for Burt's interpretation of a very delicate film of hyphae on the surface of the receptacle in *Anthurus borealis*.

Quite in contrast to Clathrus, the description of *Lysurus mokusin* shows that the volva of this plant consists of only a single layer. This layer is represented by the cortex, with a film of dried gel and the collapsed radial plates adherent to its inner surface. If one were to assert that the peripheral gel is the middle layer of the volva, he would also have to say that the most important tissue of this plant, the gleba, is a product of the volva!

Morphological Relationship between the Clathraceae and the Phallaceae

The Clathraceae and the Phallaceae are generally distinguished by two important differences: first, the development of the gleba internally to the receptacle in the Clathraceae and externally in the Phallaceae; secondly, the presence of radial plates in the Clathraceae and their absence in the Phallaceae. As already stated, *Lysurus mokusin* holds an intermediate position, resembling the Clathraceae (in *Anthurus borealis*) in its appearance and the Phallaceae in its development and the position of the gleba. The transition from Anthurus to Lysurus has not been elaborated yet, but the transition from Lysurus to the Phallaceae is described below.

The species of the Phallaceae which is most similar to *Lysurus mokusin* is *Staheliomyces cinctus* Ed. Fischer. As Fischer describes it (1921 and 1923), this fungus lacks a receptacle consisting of separate arms. The structure of the completely round stipe is maintained up to the top of the plant. The gleba lies on the outside of the stipe's upper part, but leaves its top uncovered and sterile. This sterile top corresponds to the sterile spire of Lysurus. There is only one difference—the spire of Staheliomyces is longer than that of Lysurus. Since in Staheliomyces no radial plates are developed, the gleba is not divided into separate segments, but fuses into a continuous belt.

To make the transition from *Lysurus mokusin* to *Staheliomyces cinctus*, the following suppositions are necessary: If we imagine that in Lysurus the arms, which are already almost in contact with each other, unite laterally, then we have the completely round carpophore of Staheliomyces. Furthermore, if we imagine that in Lysurus the

radial plates lose their union with stipe, arms, and spire, as well as with the cortex, and thus persist as a membrane surrounding the fruiting body, then the gleba segments would be free to fuse into a continuous belt. This structure is present in Stheliomyces. Moreover, if the radial plates are no longer attached to the stipe, the carpophore is no longer polygonal, but round, as in Stheliomyces. The basis for our last observation is the fact that the radial plates of Lysurus actually do have great ability to lose contact with the structures mentioned (see p. 62).

This hypothesis is frankly speculative, but serves at least to show that a transition from the Clathraceae to the Phallaceae through Lysurus and Stheliomyces is conceivable.

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NOTES ON ALGAE FROM THE TROPICAL ATLANTIC OCEAN. IV

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ON THREE previous occasions I have assembled short notes on marine algae of the warmer Atlantic shores of the Americas under the title above (1929, 1933, 1936). Material being available, I now offer notes on eastern American species of Microdictyon, revised descriptions of two Phaeophyceae which are incorrectly attributed in my *Marine Algae of Florida* (1928), and a list of algae from the Isla de Pinos supplementary to the long list of Cuban algae published last year (1954).

Microdictyon Species in the Curtiss Algal Herbarium

During the nineteenth century many ladies with leisure to do so assembled collections of dried plants; the botanical literature of the period abounds in references to their finds, and, dispersed in the larger herbaria, their specimens still authenticate many records. Very few of these skilled enthusiasts developed an extensive foreign correspondence among specialists, however, and their collections were rarely fated to remain together as units and in good preservation. But this was not true of the work of Mrs. Gaston G. Curtiss, generally known as Floretta A. Curtiss (Floretta A. Allen). Born in New York State in 1822 and educated there and in Ann Arbor, Michigan, Mrs. Curtiss lived for a while after the Civil War in Virginia, and finally settled, for the long remainder of her life, near Jacksonville, in Florida. There she assembled an excellent herbarium of marine algae, gathering plants locally and exchanging with J. G. Agardh and other notable students abroad; her collection consequently contains much good material from Scandinavia, South Africa, Australia, New Zealand, and elsewhere. Her prime collection, bound in albums by her son, is in the Smithsonian Institution; I am indebted to Mr. C. V. Morton, curator in charge, for the opportunity to study this material. So far as I know, Mrs. Curtiss never published any account of her work, but after her death her son wrote a

sketch of her life and activities which appeared in what is now a scarce folio pamphlet (Curtiss, 1899); thus we know more about her than we do about most amateur phycologists of the period.

It is to certain specimens in the bound collection that I want to draw attention. The genus Microdictyon of the Valoniaceae (Chlorophyceae) is represented through the West Indies, Florida, and the Bahamas by *M. boergesenii* Setchell, (Pl. I, Fig. 1), a very delicate species which is probably not extremely rare. From Cuba and the Bahamas we also have reports, though they are few, of *M. crassum* C. Ag. (Pl. II), a distinctly coarse plant about which we know little. Both species have prominent veins in the network of which the thallus is composed, and there is a tendency for branches to arise along these main vein filaments in opposite fashion. Setchell (1929) places the two species in separate sections of the genus because the fine-meshed *M. boergesenii* has simple thickened discs at the point of attachment of the branch tips in the formation of the meshes, whereas *M. crassum* is far coarser and the thickened discs are crenellate.

Both of these species attach by ordinary branch-tip cells. Setchell recognizes, however, a section called Boodleoides having a single species, *Microdictyon montagnei* from the Tonga Islands, in which, before attaching, the branch tip cuts off a special hapteral cell which becomes anchored by a crenellate disc. This hapteral cell is characteristic of several species of Boodlea, a genus that forms irregular, three-dimensional spongy masses instead of the plane blades of Microdictyon. In the Algae Curtissianae there is a specimen ascribed to the east coast of Florida which also belongs in the section Boodleoides. One always views the labels of specimens in old collections with a wary eye, but there is little chance that the origin attributed to this specimen, which I believe to belong to a species hitherto undescribed that I propose to call *M. curtissiae*, is far wrong, for the plant bears, among other epiphytes, *Fosliella lejolisii*, *F. farinosa*, and *Ceramium byssoideum*, all of them familar species of the Florida–West Indies region.

The proposed species *Microdictyon curtissiae* (Pl. I, Fig. 2; Pl. III) differs from *M. montagnei* in several ways. It has little trace of the vein system prominent in that species, but such veins as the Curtiss plant shows are about half again as wide as those in *M. montagnei*. Furthermore, the ordinary branch cells of the meshes

are about twice as wide as they are in *M. montagnei*, so that the veins do not stand out by contrast. The haptera in *M. curtissiae* are proportionately smaller—but one must guard against a discrepancy in the Setchell paper: Setchell states that the haptera in *M. montagnei* are 4–6 μ in diameter, whereas a comparison of the drawings which he published suggests that he meant to say that they were 40–60 μ in diameter, for their size bears that relation to other cells in the thallus. Both species have a slight tendency to form a few irregular meshes, which may even be out of the plane of the blade.

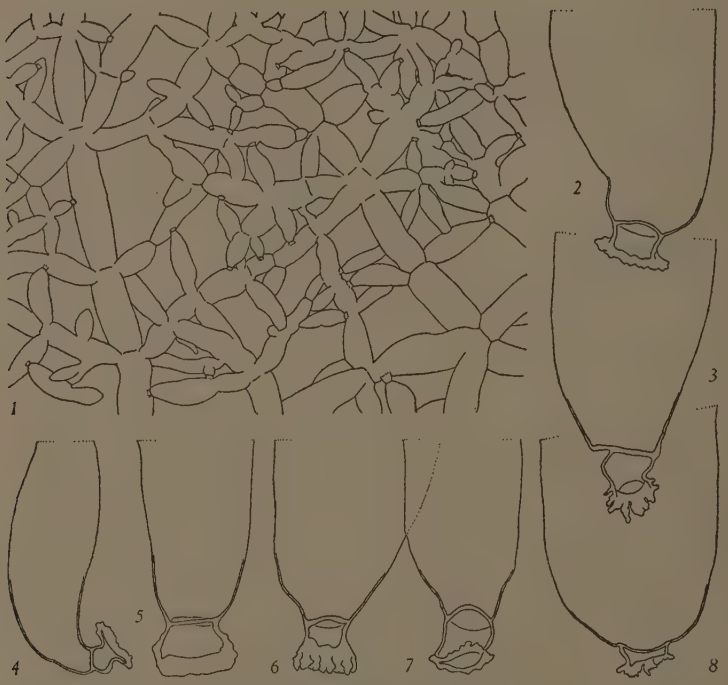
There remains the possibility that these plants may be plane-bladed boodleas instead of microdictya with hapteral cells. This becomes a matter of definition of the genera. Setchell decided that the plane blade was the most satisfactory character on which to make the separation, and I agree. As to boodleas in the American tropics, we have *Boodlea siamensis*, recorded from the Virgin Islands and Martinique, and the poorly known *B. struveoides*, from Bermuda. They differ in many features from the Curtiss plant, most tangibly in their spongy form and in being far smaller in all their parts; so our plant is clearly not one of these.

In effect, then, it appears that Mrs. Curtiss had in her collection three eastern American microdictya. Her *Microdictyon tenuius* [*sic*] from Florida is *M. boergesenii* as now understood. Her *M. crassum* came from the Bahamas and was determined by Agardh, so it is probably authentic material. A third specimen, determined only as to genus (in what seems to be Agardh's handwriting), is that described below as a new species:

Microdictyon curtissiae, sp. nov.

Planta foliacea, minime usque ad 7.0 cm. longitudine, 3.5 cm. latitudine, asymmetrice ovato-oblonga, reticulata, maculis in venas maiorum atque in maculas tenuiorum cellularum paululum discretis, venis, autem, non perspicuis; cellulae venarum maiorum ad 500–590 μ diam., 2.0–2.5-plo diam. longitudine, satis inflatae; ramificatio interdum opposita, interdum e nodo 5–6-radiata, a plano medio non manifeste deflexa; cellulae minorum segmentorum ultimatorum circa 250–340 μ diam., 2–3-plo diam. longitudine; cellulae hapterorum valde minores quam segmentum subterminale eas ferens, breves, ab extremitate proximali paululum attenuatae, 43–114 μ diam. (72 μ

diam. media), 31–82 μ longitudine (48 μ longitudine media), membrana paululum crassiore quam membrana cellularum vegetativarum, praecipue secundum marginem distalem, limbo varie irregulari aut fere fibro-crenellato.



FIGS. 1–8. *Microdictyon curtissiae*

FIG. 1. A small portion of a blade, showing maximum differentiation between meshwork and veins. × 6.5

FIGS. 2–8. Hapteral cells on the tips of seven terminal segments, showing the varying degrees of thickening and crenellation of the end membrane. × 75

On the shores of the southeast coast of Florida; from the herbarium of Mrs. Floretta A. Curtiss; collected before 1898, type now in the herbarium of the United States National Museum, Washington, D.C.

Plant foliaceous, at least up to 7.0 cm. long, 3.5 cm. broad, irregularly oval-oblong, netlike, the meshes obscurely differentiated into veins of larger and meshes of more slender cells; diameters of larger vein filaments reaching 500–590 μ, the cells about 2.0–2.5 diameters long, moderately swollen; branching sometimes opposite, sometimes 5–6-radiate from a node, the branches not clearly offset from the median plane; cells of the lesser ultimate segments about 250–340 μ in diameter, the cells 2–3 diameters long; hapteral cells markedly smaller than the subterminal segment bearing them, short, slightly tapered from the proximal end, 43–114 μ in diameter, averaging 72 μ, 31–82 μ long, averaging 48 μ, the cell wall a little thicker than that of the vegetative cells, particularly along the distal margin, where the border varies from irregular to almost fibrocrenellate. (Pl. I, Fig. 2; Pl. III; text figures 1–8.)

Revised Descriptions of Two Florida Phaeophyceae

When my *Marine Algae of Florida* was published (1928) I included with marks of misgiving two Phaeophyceae which differed from anything I knew in American waters. As time went on, I came to see even more clearly that the generic assignments were incorrect, but with only the original fragmentary specimens to work with, I could not make better assignments. Curious circumstances now enable me to revise the descriptions of these two plants. The first species was put forward as *Cladosiphon? floridana* on the basis of a well-branched piece about 6 cm. long. Some time ago I received a duplicate from the herbarium of D. C. Eaton (at Yale University) tentatively determined as Chordaria?, which, since it was labeled as having been collected by Lieutenant J. M. Ingalls, U.S.A., in "Tortugas, etc. 1873," probably came from the Dry Tortugas Islands, Florida, for Ingalls is one of the few persons who have collected algae there. Further specimens were loaned from the Eaton herbarium through the kindness of Dr. John R. Reeder, and others came from the Chicago Natural History Museum by the kindness of Dr. F. Drouet.

Ingalls' plants, which are large and in fairly good condition, quickly satisfied me that neither Chordaria nor Cladosiphon was represented by these specimens (Pl. IV). They have the structure of the Asperococcaceae, which contain a few branched genera. The radial files of surface cells that had originally seemed to me to be

assimilators are young gametangia; in sterile parts of the plant in good condition the cortex consists of a basal layer and a surface layer of taller cells covered by a cuticle. The original description mentions filaments in the medullary cavity; no filaments were found in the cavity of the distal part of this plant, but they are present near the base. Such filaments are reported by Børgesen near the base of *Rosenvingea sanctae-crucis*. Although our plants seldom branch dichotomously and are of firmer substance, they are hollow like species of Rosenvingea. The gametangia do not give rise to such prominent sori as are usual in that genus, but instead form small inconspicuous groups or are continuous over large areas. At least the end gametangial cell divides longitudinally, to show 4–12 cells in surface view. The fertile portion of the gametangium is much shorter than, for instance, what Børgesen (1914) reported for *R. sanctae-crucis*, the species our plant most resembles. Nevertheless, this genus seems the appropriate one to which to transfer our plant; my original species name is retained in recognition of its special characters.

Rosenvingea floridana (Taylor), comb. nov. (= *Cladosiphon? floridana* Taylor, 1928, p. 113, pl. 15, figs. 10–14)

The plants are dark brown, up to 32 cm. tall, sparingly branched and then chiefly near the base, without a dominant main axis; the branching is irregular, most commonly alternate but sometimes by an equal fork or opposite, with occasional aculeate projections, the ultimate segments becoming long and flexuous and having acute or, sometimes, attenuate tips. The axis diameter near the base is 0.3 mm. or even less and increases above to about 1.5 mm. Structurally the plant is essentially tubular, though sometimes it is compressed, the thallus wall being about 90–135 μ thick; the moderately thick-walled medullary cells are 45–55 (90) μ in diameter and of very considerable length; the cells of the one to three outer layers are smaller, about 20 μ in diameter; usually there are two thin-walled cortical layers, of which the inner is of rectangular cells, the outer of more or less projecting, rounded or subconical cells which are 7–10 μ in diameter, covered by a thin cuticle, and, as seen from the surface, in vague longitudinal rows. Hairs occur occasionally, slender below, above a little broader than the cortical cells or up to about 12 μ in diameter. Plurilocular gametangia are formed from the surface cells, growing out to be 3–5 cells in length, the distal of these first

enlarging a little, then dividing twice or even several times longitudinally; subsequently two or three other cells may follow suit, to form a stalked gametangium which may reach 14 μ in diameter but which is seldom twice as long as broad. (Pl. IV.)

Localities.—FLORIDA: East Key, Dry Tortugas Islands, coll. W. R. Taylor, No. *1229*, June 10, 1926, TYPE in herb. Taylor; "Tortugas, etc.," collected by J. M. Ingalls, 1873, specimens in herbaria of the Chicago Natural History Museum, Yale University, and W. R. Taylor.

The second phaeophycean that was found years ago in Florida and that I am now able to describe more fully is the one I called *Stilophora? tropica.* The original specimen is a small fragment of a mature plant, and had been rather extensively denuded. Plants recently dredged from the Challenger Bank, about thirteen sea miles southwest of Hamilton Island, Bermuda, give evidence that this plant is really a member of the genus Nereia in the Sporochnaceae, not hitherto collected from American waters. The Bermudian specimens (Pl. V) resemble *Cladothele montagnei* Kützing (Kützing, 1859, p. 32, pl. 79), which Hamel (1931–39, p. 278) considers to be synonymous with *N. filiformis* (J. Ag.) Zanard. They show how tall the American plant can grow and permit measurements to be made of all structures. In the younger sori of the Florida plant the paraphyses occupy most of the space, and the same is true for the plant from Bermuda. On the older sori there are abundant empty sporangia and few full ones, but almost no paraphyses. The cortical cells in the American plants in mature, purely vegetative regions are strongly swollen outwardly, but nevertheless are joined laterally and do not stand apart as figured by Kützing (1859, pl. 79, fig. c); my original figure (1928, pl. 19, fig. 2) reflects a condition intermediate between a vegetative region and a maturing sorus.

So far as information is available on *Nereia filiformis*, the American species seems to have much smaller paraphyses, which are composed of a single cell, whereas the European specimens have two- or, rarely, three-celled paraphyses. In addition to a Mediterranean specimen dredged by J. and G. Feldmann from 40 meters' depth off Cap Ferrat (France), in which the two-celled paraphyses measured 30–40 μ in diameter by 42–65 μ in length, I was able to examine specimens from several European localities through the kindness of Dr. D. P. Rogers, of the New York Botanical Garden, but they did

not differ widely in the size of the paraphyses. They did show, contrary to the condition in American specimens, paraphysis-like assimilators over the general cortical surface of the branches.

Nereia tropica (Taylor), comb. nov. (= *Stilophora? tropica* Taylor, 1928, p. 115, pl. 3, fig. 9; pl. 14, figs. 5, 6; pl. 19, fig. 2)

The plants exceed 35 cm. in height and are irregularly and to 2–3 degrees alternately branched; the side branches are sometimes longer than the main axis, the larger divisions being 1–2 mm. in diameter, the lesser very slender and terminating in tufts of brown filaments. The younger branches are beset at intervals with irregular, wartlike projections or spur branches, each when young bearing at the apex a tuft of brown filaments 3–6 mm. long. In young sori, paraphyses and sporangia are crowded about the base of the hairs. Older sori may grow out into spur branches and then the paraphyses and sporangia lie behind the tuft of hairs, though the oldest sori and spurs become depiliate. The main axes are terete, with a wide medulla of cells, of which the center ones may reach a diameter of 110–220 μ and have slightly thickened walls, whereas the outer ones are smaller, about 12–20 μ in diameter, and have thicker walls; the cortex is composed of a single layer of outwardly swollen, thin-walled cells 15–70 μ broad in section and 18–40 μ tall. The hairs which terminate leading axes, spur branches, and sori are 17–26 μ in diameter, and the cells reach a length of 3–9 diameters. The paraphyses are crowded on the younger sori; they are composed of broadly clavate or obpyramidal cells narrowed into a stalk and are 17–28 μ in diameter and 32–51 μ tall. The sporangia are usually borne two or three or more on the same basal cell with one or two paraphyses, and are subcylindrical to obovoid, 11–19 μ in diameter, 26–42 μ long. (Pl. V.)

Localities.—Florida: Dry Tortugas Islands, dredged from 9.2–14.6 meters' depth in Southwest Channel, coll. W. R. Taylor, No. 674, June 11, 1925, type in herb. Taylor. Bermuda: dredged from the Challenger Bank at 52 meters' depth, coll. H. Lowenstam, Aug. 18–19, 1953, communicated by W. H. Sutcliffe, Jr.

Additional Records of Marine Algae from Cuba

In a recent paper (Taylor, 1954) I reported many new localities for marine algae in Cuba, including numerous species recorded for

the first time from the Republic. A considerable further collection made by Dr. E. P. Killip on the Isla de Pinos (Province Pinar del Río) during February and March 1953 having come to hand, I am able to add a few new records for that island, which, because of its size and isolation, is worthy of particular attention. With the exception of one paper by Jennings (1917) that includes Isla de Pinos algae, the special literature on Cuban seaweeds may be reached through the article already cited (Taylor, 1954).

CHLOROPHYCEAE

VALONIACEAE

Cladophoropsis membranacea (C. Ag.) Børg.—Playa Columpo, Killip *42639*, *42642*, *42645;* Playa de Herradura, Killip *43173*.

CAULERPACEAE

Caulerpa cupressoides (West) C. Ag.—Playa Columpo, Killip *42806*.

Caulerpa sertularioides (Gmel.) Howe.—Playa Columpo, Killip *42638*.

CODIACEAE

Halimeda tridens (Ell. & Sol.) Lamx.—Playa Columpo, Killip *42984*.

PHAEOPHYCEAE

DICTYOTACEAE

Dictyota cervicornis Kütz.—Playa de Herradura, Killip *43179*.

Dictyota dichotoma (Huds.) Lamx.—Playa de Herradura, Killip *43174*, *43178*.

RHODOPHYCEAE

CORALLINACEAE

Corallina cubensis (Mont.) Kütz.—Playa de Bibijagua, Killip *43123;* Playa Columpo, Killip *42644*.

Fosliella farinosa (Lamx.) Howe.—Playa Columpo, on Laurencia, Killip *42643* (in part).

Jania rubens Lamx.—Playa Columpo, on Digenia, Killip *42648* (in part).

HYPNEACEAE

Hypnea musciformis (Wulf.) Lamx.—Playa Columpo, Killip *42803*, *43184*.

DASYACEAE

Heterosiphonia gibbesii (Harv.) Falk.—Playa Columpo, Killip *42647;* Playa de Bibijagua, Killip *43121;* Playa de Herradura, Killip *43176*.

RHODOMELACEAE

Chondria atropurpurea Harv.—Playa Columpo, Killip *42802*.

Laurencia papillosa (Forssk.) Grev.—Playa Columpo, Killip *42640*, *42641*.

Laurencia poitei (Lamx.) Howe.—Playa de Bibijagua, Killip *43119*, *43120;* Playa de Herradura, Killip *43156*.

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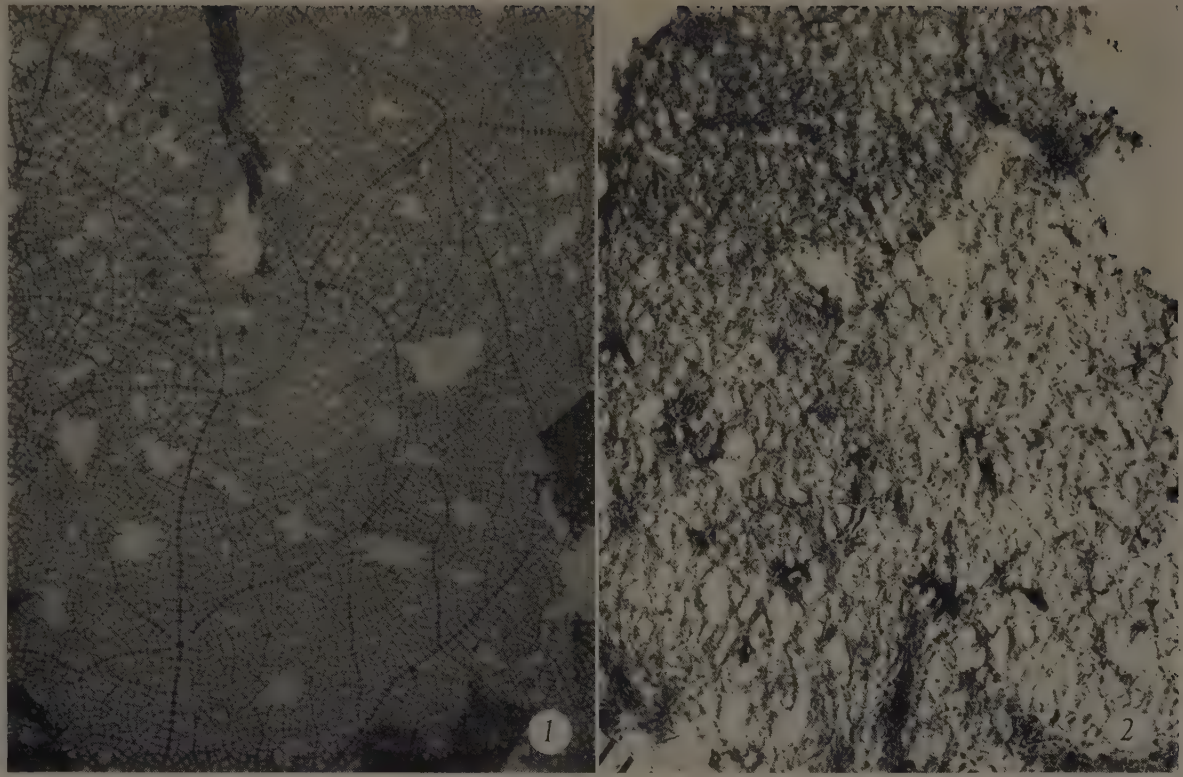
University of Michigan

PLATES I–V

EXPLANATION OF PLATE I

FIG. 1. *Microdictyon boergesenii*, a small portion of a blade, showing the general delicate meshwork and veins. × 40

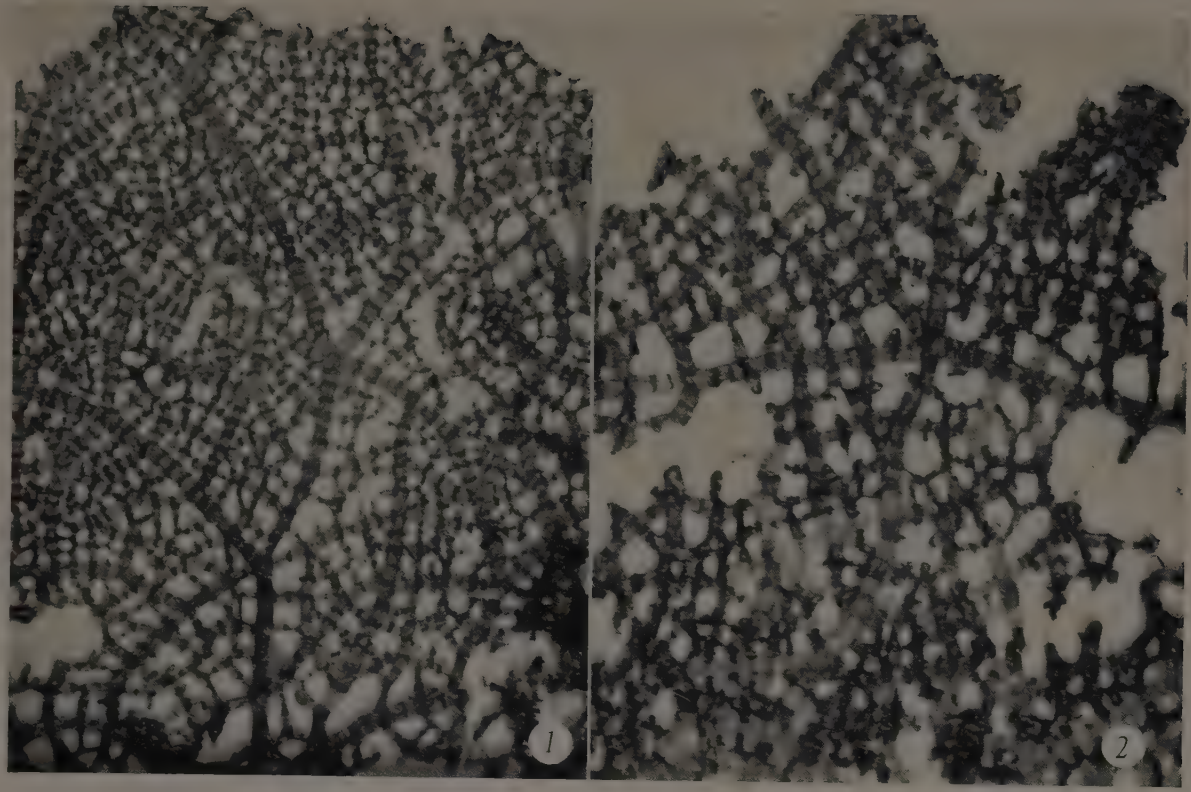
FIG. 2. *M. curtissiae*, a small portion of a blade, showing the general rather coarse meshwork (since the specimen was completely decolorized, it was difficult to secure a good photograph). × 38


1
2

EXPLANATION OF PLATE II

FIG. 1. *Microdictyon crassum*, a small portion of a blade, showing the general very coarse network and veins. × 40

FIG. 2. *M. crassum*, a further enlarged detail, showing the cell proportions in veins and meshwork. × 50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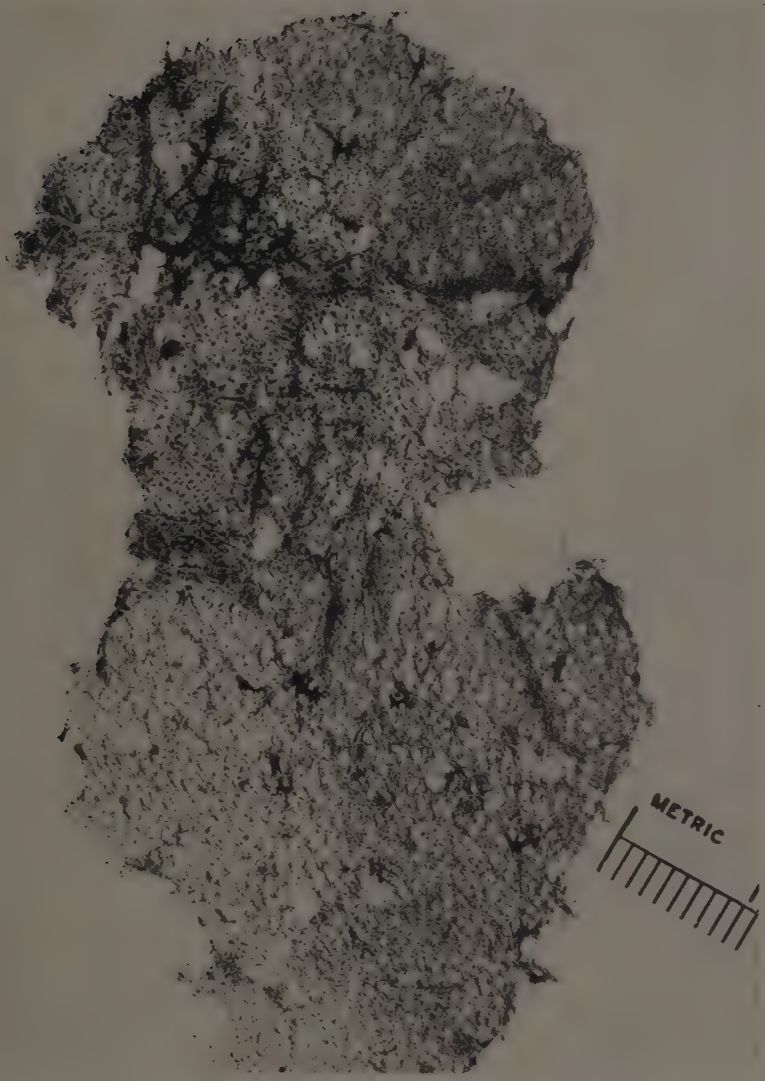
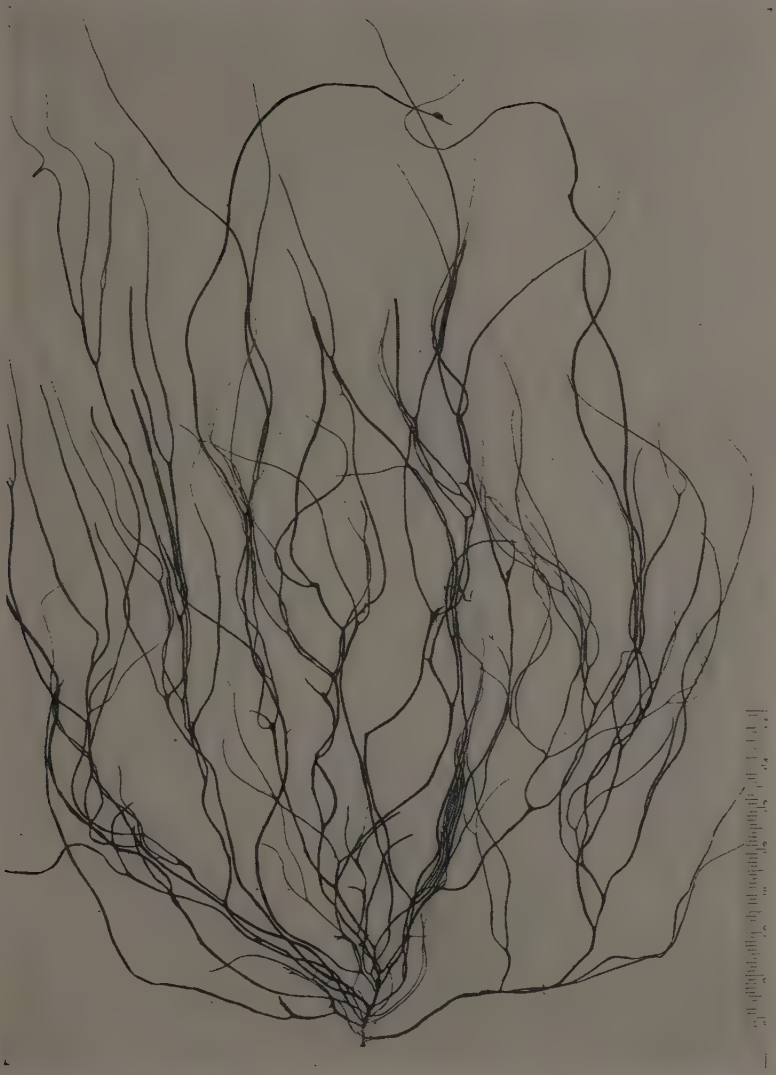


Microdictyon curtissiae, type specimen, general view showing absence of conspicuous veins. × 23.5



Rosenvingea floridana, general view of a large specimen in the herbarium of the Chicago Natural History Museum, collected by J. M. Ingalls in the Dry Tortugas. × 0.6

Nereia tropica, general view of the upper branching of a specimen from the Challenger Bank collected by H. Lowenstam. preserved in formalin and later stained and mounted. × 0.6

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EVALUATION OF SPECIFIC CHARACTERS IN THE GENUS TULOSTOMA PERS.*

JORGE E. WRIGHT†

AMONG the Gasteromycetes, and particularly in the genus Tulostoma, there seems to be a good deal of discrepancy concerning the delimitation of species. This is apparently due to the lack of a world-wide knowledge of the members of any single genus, on the one hand, and to the very few reliable morphological features that can be used for the separation of the species, on the other. It is also recognized that while the genera of the Gasteromycetes offer in most cases conspicuously well-defined characters, the species in the majority of the genera are difficult to separate.

As an outgrowth of my study of the Gasteromycetes of South America, I became interested in the genus Tulostoma on a world-wide basis. From materials so far examined, certain conclusions in regard to the value of characters at species level may now be drawn. The following, in the order of their importance, are the features considered to be most reliable for the delimitation of species of Tulostoma.

Mouth.—From my studies I am able to recognize only two main types, *definite* and *indefinite*.

A definite mouth is one that can easily be seen to be a mouth, whatever its nature may be, and that is readily differentiated from the rest of the spore case. This type of mouth, when present, is

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observed in most well-preserved collections without any difficulty; it varies within reasonable limits and thus constitutes the best means of separating the species into groups. It may be *tubular*, in which event the opening is flat, usually has a small lip, but sometimes does not, and is always circular to elliptical in shape, even, and very distinct. Or it may be *fibrillose*, and then it appears as an opening in a slightly raised, more or less marked, fibrillose region, at times being shield-shaped and colored or uncolored, but never in the least tubular. Most species fall into one of these two groups having definite mouths.

An indefinite mouth is a flat orifice, not always in the center of the spore case; it is very seldom round, being just an opening, and it is never surrounded by a lip or a fibrillose zone. It is always concolorous with the rest of the endoperidium. Were it not for a well-defined socket on the lower part of the spore case and for various microscopical details, the species with this type of mouth might be classified as members of the Schizostomae; a good example of this possibility is afforded by *Tulostoma obesum*.

Workers coming immediately after Persoon, and all those who have taken up the subject in modern times, are agreed that the best character for grouping the species into sections (subgenera of various authors) is the configuration of the mouth. Up to the first decade of the present century investigators recognized what appear in Saccardo's *Sylloge fungorum* (Vol. VII, 1888) as Eutylostoma and Schizostoma. The latter, however, had been segregated by Léveillé (1846) on the basis of the differences in capillitium, but it was really Lloyd (1906) who stressed the validity of these differences between Schizostoma and the true Tulostomae. Some modern workers do not accept this distinction (Fischer, 1933).

Not all authors agree as to the number of mouth types that may be found in the genus Tulostoma. Thus Lloyd (1906) establishes five types, which he calls "tubular," "irregular," "torn," "fibrillose," and "fimbriate," and Long and Ahmad (1947) also define five types, which they designate "tubular," "subfibrillose to indefinite," "valvate," "operculate," and "indefinite." When working with the species it at once becomes obvious that such classifications are untenable on practical grounds; I am more inclined to rely on the two main types defined above.

Furthermore, such terms as "fimbriate," "valvate," and "opercu-

late" can apply only to stages of development; the fibrillose mouth of *Tulostoma exasperatum*, for example, may assume a valvate appearance in the dehiscent stage, the tubular mouth of *T. operculatum* may have an operculum or lid when young, and so on.

Spores.—The spores were critically studied with the aid of the best magnification obtainable under oil immersion, and their details were carefully observed. Water, KOH, and Melzer's iodine reagent were employed as mounting media. It is usually necessary to wet the spores with a 70 per cent alcohol solution to decrease the surface tension. Under these conditions it was found that two kinds of spores occur in Tulostoma, viz., *smooth* (Fig. 1 *a* and *f*) and *ornamented*. One may occasionally find among large numbers of perfectly smooth spores, some that appear to be very slightly angular, but I do not believe this fact has any bearing on the type of ornamentation of the particular species. I have seldom had any difficulty in judging whether the spores were or were not smooth.

Among the ornamented spores there are two parallel series, one correlated with the tubular mouths (Fig. 1 *b–d*), and the other with the fibrillose mouths (Fig. 1 *g–j*). The first series runs from *asperulate* ("punctate" of some authors), through *verrucose* (Fig. 1*b*), to *echinulate* (Fig. 1 *c–d*), and the second from *asperulate* (Fig. 1*j*), through *verrucose*, *echinulate*, and *reticulate*, to *striate* (Fig. 1 *i* and *h*). It should be stated here that qualifying words for these types are often urgently needed.

It would thus appear that a continuous sequence exists in the complexity of spore ornamentation. This is exemplified by my findings on the striate type. Collections from as different localities as Australia, the United States (both east and west), Paraguay, and Argentina, practically undistinguishable in their external morphology, showed the same type of ornamentation in the most striking range. These spores were slightly striate in some specimens, had more pronounced "ribs" in others, and in a few instances[1] showed rings arranged in approximately the same relationship as the polar circles bear to meridians. At the distal end the striae cross at different planes and, in consequence, the spores look quite unequal (Fig. 1*h*).

[1] It is a curious fact that the collections showing the most conspicuous striae are from high altitudes, one of them being from a spot near a mine in the Andes, Province of Jujuy, Argentina.

FIG. 1. Microscopic characters of Tulostoma: *a*, Spores and capillitium of *T. longii*; *b*, spores and capillitium of *T. brumale*; *c*, spores of *T. bonianum*; *d*, spores and capillitium of *T. verrucosum*; *e*, spores and capillitium of *T. fulvellum*; *f*, spores and capillitium of *T. lloydii*; *g*, spores and capillitium of *T. macowanii*; *h*, spores and capillitium of *T. striatum*; *i*, spores and capillitium of *T. exasperatum* (lower right spore corresponds to the form found in *T. ridleyi*, type specimen in Royal Botanic Gardens, Kew, England); *j*, spores and capillitium of *T. berteroanum*; *k*, "mycosclereids" from outer layer of endoperidium of *T. berteroanum*

Just one species with striate spores has been found, namely, *Tulostoma striatum*, which Cunningham (1925) described from Australia. It had been reported only once from the United States (Smith, 1951), but I have discovered it to be of rather frequent occurrence in this country, both in the east and in the west; it has also been collected in Paraguay (as *T. berteroanum* Lév., in Royal Botanic Gardens, Kew, England) and in Argentina, near the Andes in the provinces of Mendoza and Jujuy.

Size is another characteristic of the spores that is a valuable datum at the species level, although in Tulostoma it is difficult to establish size groups, in spite of the regularity of the measurements found in the different species. Size can be utilized, however, to separate species with small spores (usually up to 4 μ) (Fig. 1*e*) from those with larger ones (usually from 5 to 7 μ) (Fig. 1 *d*, *h*, *i*). Several species with very large spores can immediately be recognized by this feature.

There has been a great deal of argument concerning the usefulness of microscopical information in the Gasteromycetes, and all who work with the group have aligned themselves on one side or the other. Lloyd's authority seems to have been taken as sufficient by many investigators, who followed him in his disregard for such features. One of the more recent advocates of this attitude was the late W. H. Long, who expressed the opinion that the separation of species on spore characters was "futile." To support his viewpoint he mentioned the error incurred by Cunningham (1942)—who is of the opposite opinion—when he reduced to synonymy three species, *Tulostoma obesum*, *T. poculatum*, and *T. lloydii*, which are quite dissimilar and, in point of fact, may even be distinguished on sight.

Petri (1904a, 1904b) was the first to call attention to the usefulness of both capillitium and spore characters for the identification of the species of Tulostoma, although Miss White (1901) had keyed out, somewhat earlier, the North American species on the basis of these elements. In Volume XVII of his monumental work, Saccardo (1905) duly incorporated a modified version of Petri's keys. It is unfortunate that Petri seems not to have had a sound knowledge of the species of the Western Hemisphere, where so many widely diverse forms occur; this fact, added to Lloyd's contempt for his work, caused Petri's papers to be neglected by a great number of investigators.

Those who are familiar with modern work in the Agaricales will not fail to recognize that the use of microscopical characters and, especially, of spore ornamentation, has contributed greatly to the advance in our knowledge of the group during the first half of this century. The critical use of microscopic characters in the Gasteromycetes in general, and in the genus Tulostoma in particular, will afford, in my opinion, a more reliable structure for the delimitation of species. It must be exercised, nevertheless, with the greatest care.

It should be pointed out that many collections will have to be reëxamined in regard to spore character, since their previous identification may be incorrect; this will naturally have a bearing on our knowledge of the geographical distribution of the members of the genus.

Capillitium.—The capillitium, notwithstanding Petri's work on the subject (1904b), is, in my opinion, of only secondary importance so far as the delimitation of the species is concerned, and it should always be considered in conjunction with the spore type. It is obvious that there exist capillitium types, but these need further study. I agree with Petri that it is possible to distinguish two main types, viz., *colored* and *uncolored* or *hyaline.* But here only extremes can be relied upon; there are too many intermediates. Only a few species have what may truly be termed a colored capillitium; a typical example is *Tulostoma obesum.*

The nature of the septa is, perhaps, a more useful character, since it is possible to establish—as Petri did—whether the threads may or may not be disjointed. Threads with rounded ends ("knotty" at the septa) are easily disjointed and are usually uncolored (Fig. 1 *a* and *e*). Threads that are not easily disjointed are of two general types: (1) the ends of the threads are abruptly and conspicuously thickened at the septa, and then they are generally intensely colored (Fig. 1 *b* and *j*); (2) the ends are only slightly thickened and the septum proper is colored (Fig. 1 *d* and *g*).

It is sometimes hard to observe a sufficient number of septa to judge their nature, and I believe it is worth while to point out in this connection that if one studies the microscopical structure of the endoperidium walls, one may find there the corresponding capillitium type, but *usually uncolored.* The endoperidium walls seem to be made up in most instances of threads which are closely similar in nature to the capillitium, the septa being very numerous. It is not

known that this character has ever been utilized before for taxonomical purposes.

ENDOPERIDIUM.—The endoperidium is perhaps the second-best gross morphological feature that can be used in the recognition of species of Tulostoma.

Lloyd (1906) stressed the presence or absence of color (peridium *colored* against peridium *uncolored*) of the endoperidium. This seems a good criterion, and I am adopting it with a slight modification, that is, I distinguish between a *light-colored* and a *dark-colored* endoperidium, since most endoperidia have some hue.

No attempt has previously been made, however, to correlate macroscopical and microscopical features of the endoperidium; this appears to be a new approach in the search for more outstanding elements for specific diagnoses. I have found that in one case, at least, namely, in *Tulostoma berteroanum* Lév., conspicuous thickened and colored terminal hyphae are constantly present in the external portion of the walls of the endoperidium. On account of their peculiar shape, which at first reminded me of the giant sclereids found in higher plants, I have tentatively given them the name "mycosclereids" (Fig. 1*k*). I ruled out the term "setae" because of the dissimilarity between these hyphae and the setae found in the Polyporaceae and other groups. This discovery indicates the need of further research on this character in all the known species.

Furthermore, the degree and nature of persistence of the exoperidium on the endoperidium furnish an additional useful character, when employed with caution (compare *Tulostoma exasperatum*, *T. bonianum*, and *T. verrucosum*).

EXOPERIDIUM.—This element has proved a reliable element in only a few cases (*Tulostoma exasperatum*, *T. leveilleanum*, and one or two others). After having examined several hundred collections, I am convinced that it is not possible to distinguish more than two different types of exoperidia, viz., *granular* and *membranous*.

The granular type consists in an agglutination of hyphae and sand particles; it wears off, leaving a cuplike structure at the base of the spore case surrounding the socket; in some instances, it assumes characteristic proportions. The spore case has then been described as of "acorn-cup" appearance. This sort of exoperidium is found typically in sand-inhabiting species.

The membranous type consists of a membranaceous layer, usually

whitish within and dark outside, which peels off from the apex downward, but sometimes remains attached to the endoperidium in patches. It is found typically on clay-inhabiting species, or in the so-called forest Tulostomae.

Some authors have placed considerable emphasis on the nature of the exoperidium. Long (1944, 1947) and Long and Ahmad (1947) proposed the following classification of exoperidia in Tulostoma: "granular" (consisting of hyphae and sand), "semimembranous," "permanently membranous," and "hyphal." Although it may be possible to distinguish two, or even three, of these types in young specimens in which the exoperidium is complete, the majority of collections are made up of mature specimens in which it has receded and appears merely as a cup at the base of the spore case. It is usually very difficult to discern the nature of the outer peridial layer.

Here again detailed microscopical study—which has not been undertaken so far—might furnish an additional datum.

Stipe.—This organ was widely used by older authors in basing new species. If the great degree of variation which it offers could be accounted for, it would be judged a good character. As this has not been done, however, it must be employed critically. The stature and color (peeled and unpeeled) and the markings that are not of an ephemeral nature (viz., the striations) are fairly reliable. The fibrils, squamules, and other similar adornments must be used carefully, and too much stress must not be laid on them. The facility with which the stipe separates from the spore case seems to have some taxonomical meaning, provided it is correlated with other characters. It has not been used to any extent except by Long.

Collar.—What has been said of the stipe applies equally well to the collar. The degree of separation from the stem is too variable to give much information, but in general two types of collar are found: *distant* and *close*.

The membrane which remains in the socket when the stipe elongates, and which might be termed the collar proper, is in many instances a valuable secondary character. It may be *inconspicuous* or *distinct;* if it is distinct, three general types exist: *simple*, *indented* (denticulate, grooved, and so on), and *pendent*. A simple collar membrane is one which does not show any indentation, whereas the indented one may have grooves, may consist of small, pointed squamules, or may be irregularly torn. The pendent collar mem-

brane is conspicuously squamose and colored (as in *Tulostoma rickii*). This type is found more generally in the tropics.

HABITAT.—As with many other plants, habitat is of a certain diagnostic importance in Tulostoma; but it has generally been overlooked by authors. Long and Ahmad (1947) discussed this aspect in some detail. One is not likely to find a sand-loving species on clayish soil or a clay-loving species on sandy soil. Only one species has been recorded as growing on wood (*T. leveilleanum*), and further proof of this habitat is required.

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FORESTRY

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SOME RESUPINATE POLYPORES FROM THE REGION OF THE GREAT LAKES. XXVI*

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THE polypores that cause the greatest decay losses in standing timber and in timber products in the Lake States region are believed to be widely distributed over North America. Only incomplete data pertaining to the specific ranges of these fungi are actually available, however, since few adequate systematic attempts to sample the vast continental forests for fungi have been reported.

In the effort to learn about the incidence of the polypores within the vegetative formations and forest associations, collections have been made by me in every state in the Union, in Alaska, in every Canadian province, including the newly added province of Newfoundland (Labrador and Newfoundland), in the Yukon Territory, and in the Northwest Territories.

This paper discusses the occurrence of some of the important polypores of certain forests and also their incidence in diverse east-

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ern and northern vegetative associations. In contrast to the fungi that thrive best under forest conditions is a group of polypores commonly found in environments where particular wood products are in general use. *Poria vaillantii* (Fries) Cooke on timbers in greenhouse benches is an example. This fungus, known from only thirteen states, is described from Michigan in the present account.

The Occurrence of the Ubiquitous Polypore Fomes pini with Reference to Forest Associations

Fomes pini is one of the fungi of the Lake States region that are classed as ubiquitous.[1] Collections have been made in forty-five states, the District of Columbia, eleven Canadian provinces and territories, and Alaska. It is known, therefore, from fifty-eight political divisions. Only *Lenzites saepiaria*, *Polyporus abietinus*, *Pol. adustus*, and *Pol. pargamenus* are more widely distributed, with sixty-one such areas recorded for *L. saepiaria* and sixty for the others. Furthermore, in addition to being widely distributed in North America, *F. pini* attacks a great number of kinds of substrata on this continent. I have records of it on fifty-eight species of wood.

In spite of its ubiquitousness, however, the fungus exhibits marked differences in occurrence within a forest region. It has been shown (3) that in Oregon Douglas fir, for example, *Fomes pini* is most abundant on sites with southerly aspects. Since timber growing in such localities is subject to much cull due to decay, it is obvious that forest practices in regard to green standing timber will depend upon the amount of defect on the sites; because of the varied incidence of the fungus, or of other fungi, even within a forest composed wholly of one species, differential treatment of the various sections will be required.

Records of incidence of *Fomes pini* and of other fungi in Alaskan forests have been obtained during fifteen field seasons. Although information concerning the abundance of *F. pini* on slopes with southerly aspects is lacking, our studies indicate that its frequency varies greatly with the locality. In spite of its wide range, it is not generally distributed in the northern coastal coniferous forest, and it appears to be less important the farther north one travels in the

[1] Ubiquitous species are defined here as those fungi that have been described in the great majority of the states of the Union, in the majority of the provinces and territories of Canada, and in Alaska.

forest of the Alaskan Panhandle.[2] To the westward, in the coastal Alaskan forests, however, *F. pini* is abundant (2).

Furthermore, it is often held that in the United States the presence of *Fomes pini* may be correlated with the age of the timber: If the timber is overmature, *F. pini* will be present. Such a relationship is not so apparent in many of the northern coastal districts—the Yakutat area in Alaska, for example. Here this fungus was not found to be the chief cause of decay on western hemlock–sitka spruce forests that were from four hundred to five hundred years old. Cull due to other causes, however, may be high. In fact, another fungus, *F. pinicola*, leads to more cull in green standing conifers in this area than in such timber in forests in the States. It is evident that factors other than the kind of forest association account for the occurrence and the abundance of ubiquitous fungi such as *F. pini*.

The Occurrence of Nonubiquitous Polypores[3] in Certain Eastern Forests of North America

Efforts to find a means of identifying fungi that cause decay in wood or in a restricted habitat have resulted in a number of important studies of these organisms in culture, but the features of many of the lignicolous fungi are still unknown. An excellent key (and perhaps the largest one available) has been prepared by Nobles (6). It accounts for over one hundred plants, but even this, as Dr. Nobles mentions, is a small group in comparison with the number of species of wood-rotting fungi that may occur. Awareness of both the

[2] The presence of *Fomes pini* in the interior forests of Alaska does not follow the pattern observed in the coastal southeastern timberlands. I have collected it far north in interior forests. It has also been found to be common on coastal sites west of the Yakutat areas and on sites still farther westward, to the limit of Sitka spruce growth on Kodiak Island.

[3] The resupinate fungi reported below include those pileate species that often become resupinate. In several forest types resupinate forms are more common than pileate. The list presented here does not represent the total number of polypores that are known to attack the species indicated. The complete index is much greater and will be published later. The present list represents the nonubiquitous fungi that have appeared again and again in collections made in the various association types, or, in other words, the fungi that may be considered "key" or "index" species. It accounts for the majority of the species most likely, though not inevitably, to be found wherever the association occurs on the continent. The ubiquitous species (defined in footnote 1) are omitted so as to emphasize the forms characteristic of various environments.

ubiquitous and the nonubiquitous polypores that may be found in a given type of forest association should be helpful in making tests and in arriving at determinations in particular instances. *Poria crustulina*, for example, is almost certain to be present on dry sites where spruce is a component of the vegetative association.

An index of hosts and substrata for the polypores[4] indicates that for the most part the same fungi are known on woods of generally similar structure and occurrence, and it can be observed in vegetative associations which are distinguished chiefly by the expression of dominance of one or another of the tree species present that a large number of the same fungi recur. The particular dominance, however, may be a factor in the abundance of certain fungi within the forest. For example, a list of the polypores recorded on *Pinus banksiana* is almost the same as that for *P. resinosa* (see below, pp. 98–99). However, the number of fungi obtained and some of the species observed in a red pine and a jack pine forest may differ. This is probably because of variations in moisture in the two forests and because the soils of the red pine stand are somewhat superior to those of the jack pine stand. Soils in the red pine forest are likely to support a larger number of secondary arborescent species. The secondary species often contribute in turn to the number and kinds of fungi that frequent the association.

Most of the polypores found in the climates of the Great Lakes occur, at least on occasion, in the majority of the vegetative zones of the continent. These climates provide both hardwoods and coniferous woods as potential hosts and substrata for the fungi. Certain polypores from other vegetative zones do not occur, however, in the region of the Great Lakes. *Polyporus corrosus*, *Pol. ectypus*, *Pol. hydnoides*, *Pol. sector*, *Poria borbonica*, *P. bracei*, *P. heteromorpha*, *P. flavomarginata*, *P. limitata*, and *Trametes subserpens*, for example, are found only in southern vegetative types (see pp. 102–104, southern cypress–hardwood, pond pine, and live oak–cabbage palmetto associations). Since most of these fungi may occur in the Gulf States on wood species that grow farther north, it appears that there is some correspondence of the species of polypores with the climatic environment. The presence of specific hosts or substrata

[4] Host and substrata lists for the North American resupinate polypores are contained in an unpublished manuscript of mine in the School of Natural Resources, University of Michigan.

peculiar to a few polypores (for example, the *Sabal palmetto* palm for *Poria heteromorpha*) is likewise largely a response to climate. Variations in soils affect the local distribution of the host and substrata plants.

From the record of collections made, it can be seen that there is a significant difference both in species of polypores present and in their abundance in timberlands growing in either very wet or very dry sites and in those growing under more favorable conditions as to moisture (p. 103, water oak–red gum association). On both the very wet sites (southern white cedar forest) and the relatively dry sites (post oak–black jack oak association) only nine or ten fungi are listed in addition to the ubiquitous species. If the association is northern and consists largely of spruce on a relatively dry site, *Poria crustulina* and *Polyporus abietinus* are the two most characteristic fungi. On sites with more favorable conditions of moisture (white spruce–aspen–birch, often with balsam) there may be present as many as twenty-nine polypores, exclusive of those that are ubiquitous.

Variation in incidence and, especially, in abundance of the particular kinds of polypores present in different climatic environments where the same or closely related species of the host genus are involved is likewise evident from the data present here (p. 96, northern poplar type and the more southern cottonwood association). Attention is called to the occurrence of *Poria tacamahacae* and *P. ambigua* in the northern and the southern North American cottonwoods. *P. tacamahacae* is almost certain to be found in poplar forests of the Lower MacKenzie River in the Northwest Territories and the Yukon and in poplar forests of other northern streams. The fungus is by no means so abundant and often does not occur at all in the cottonwood forests along the southern Mississippi River. *P. ambigua*, on the other hand, is present in almost all the cottonwood forests of the overflow lands near St. Louis, Missouri, and southward to the Gulf of Mexico.

Eastern Forest-Site Relations for the Nonubiquitous North American Polypores

The list below includes the eastern black and white spruce associations that extend westerly across the continent into the Yukon Territory and Alaska.

Poplar (*Populus spp.*, chiefly *P. tacamahaca*)

Secondary associates.—Willow, *Salix spp.;* alder, *Alnus spp.;* white spruce, *Picea glauca.*

Sites.—Low, often inundated, river bottoms and swamp borders, especially islands and river banks. Labrador to latitude 65° north in the valley of the MacKenzie River and to the Alaskan coast, south to northern New England and New York, central Michigan, the Black Hills of South Dakota, and along the streams of the Prairie region of northwestern Canada.

Resupinate polypores.—*Fomes igniarius, Polyporus caesius, Pol. dichrous, Pol. hirsutus, Pol. stereoides, Pol. velutinus, Pol. zonatus, Poria aneirina, P. corticola, P. punctata, P. resinascens, P. tacamahacae, P. unita pulchella, P. xantha, Trametes hispida, T. suaveolens.*

Fomes igniarius is ubiquitous for Alaska and the Canadian territories and provinces, but not for the entire continent. It is known from only thirty-two states in the United States.

Poria unita pulchella is one of the most common polypores in the aspen forest of the Cassiar as well as in parts of the Yukon. It becomes a serious problem on aspen fence timbers, which are in common use in northern sections of the district and the Territory.

Cottonwood (*Populus spp.*, chiefly *P. deltoides*)

(Pl. I)

Secondary associates.—Pure, or with black willow, *Salix nigra;* peach-leaf willow, *S. amygdaloides;* sand-bar willow, *S. longifolia;* box elder, *Acer negundo;* silver maple, *A. saccharinum;* hackberry, *Celtis occidentalis;* red gum, *Liquidambar styraciflua;* American elm, *Ulmus americana.*

Sites.—Moist soil, stream banks, sand bars, *batture* lands, and islands in larger water courses. Province of Quebec south through western New York and Pennsylvania, westward to southern Minnesota, North and South Dakota, eastern Kansas, and Oklahoma, the Gulf States and Texas.

Resupinate polypores.—*Polyporus caesius, Pol. radiatus, Poria ambigua, P. corticola, Trametes hispida.*

Black Spruce (*Picea mariana*)

Secondary associates.—Pure, or in parts of its range with some white cedar, *Thuja occidentalis;* balsam, *Abies balsamea;* tamarack, *Larix laricina;* black ash, *Fraxinus nigra;* red maple, *Acer rubrum;* paper birch, *Betula papyrifera.*

Sites.—Poorly drained, cold, acid bogs and peat swamps (called "muskegs" in Alaska and northern Canada) common, but continually moist alluvial soils most favorable. Transcontinental —Labrador to the MacKenzie River and northwestward into northwest Alaska as far as the mouth of Noatak River. In eastern North America, south through Newfoundland and eastern Canada to central Pennsylvania; in the mountains of northern Virginia and in the Lake States.

Resupinate polypores.—Fomes conchatus, F. connatus, F. pini abietis, F. pinicola, F. roseus, Polyporus anceps, Pol. balsameus, Pol. glomeratus, Pol. radiatus, Pol. semisupinus, Pol. stereoides, Poria crustulina, P. ferrea, P. inermis, P. obliqua, P. papyracea, P. punctata, P. subfuscoflavida, P. tacamahacae, P. undata, Trametes hispida, T. malicola, T. mollis, T. odorata.

White Spruce (*Picea glauca*)
White Spruce–Aspen (*Populus tremuloides*)
White Spruce–Willow–Balsam Fir–Paper Birch (*Salix spp., Abies balsamea, Betula papyrifera*)
White Spruce–Lowland Fir (*Abies grandis*)
White Spruce–Western White Birch (*Betula papyrifera* or *B. papyrifera kenaica*)

Secondary associates.—White spruce in pure (frequently) or mixed stands as indicated, or associated also with the aspen *Populus grandidentata* (Pl. II) (*P. tremuloides* is often abundant enough to form a forest by itself; see Pl. III); or, in the far north, with tacamahac, *P. balsamifera;* or black spruce, *Picea mariana;* or tamarack, *Larix laricina;* or, in the east, with red spruce, *P. rubra;* and, in the foothills of the Canadian Rockies (Alberta) and in British Columbia, with Engelmann spruce, *P. engelmannii;* or white birch, *Betula papyrifera occidentalis.*

Sites.—Characterized by great variation in soils, from margins of swamps to very dry soils (as in sections of the Yukon Territory) and mountain tops; but moist, well-drained alluvial soils, lower benches, gravelly soils, and slopes bordering rivers most favorable; in the north, soil often frozen, beneath first surface foot or two, for the entire year. Labrador to Hudson Bay and northward through Alaska to Bering Straits; in the Atlantic area southward to Maine and northern New York and in the Great Lakes area westward to Montana, South Dakota, and British Columbia.

Resupinate polypores.—*Fomes igniarius, F. pini abietis, F. pinicola, F. roseus, Polyporus alboluteus, Pol. anceps, Pol. dichrous, Pol. fragilis, Pol. mollis, Pol. pubescens, Pol. radiatus, Pol. semisupinus, Pol. stereoides, Pol. velutinus, Pol. zonatus, Poria albobrunnea, P. aneirina, P. coniferarum, P. corticola, P. crustulina, P. eupora, P. ferrugineofusca, P. laevigata, P. luteoalba, P. obliqua, P. tacamahacae, P. xantha, Trametes heteromorpha, T. variiformis.*

Fomes igniarius (aspen form on *Populus grandidentata* illustrated in Pl. II) attacks birch in an aspen forest. This is the most noteworthy example of the aspen form of *F. igniarius* on a host other than aspen that is recorded in my field data for the entire continent. The fungus is less abundant in the cottonwood forests growing along the big northern rivers than it is on aspen.

Jack Pine (*Pinus banksiana*)

(Pl. IV)

Secondary associates.—Pure in large stands, or with red pine, *Pinus resinosa;* paper birch, *Betula papyrifera;* pin cherry, *Prunus pennsylvanica;* red oak, *Quercus maxima;* and jack oak, *Q. ellipsoidalis.*

Sites.—Barren, sandy soils, as well as rocky ledges or moist sands near swamps, mostly outwash plains. Nova Scotia south to northern New Hampshire, Vermont, Massachusetts, and northern New York; west through the region of the Lake States and southern shores of Hudson Bay to Great Bear Lake and MacKenzie River (see Pl. IV, *Pinus banksiana–Picea glauca–Betula papyrifera*).

Resupinate polypores.—*Fomes igniarius, F. pini abietis, F. pinicola, Polyporus anceps, Pol. gilvus, Pol. rutilans, Poria corticola, P.*

rixosa (considered an index species), *P. subfuscoflavida*, *P. unita pulchella*, *P. xantha*, *Trametes carbonaria*, *T. hispida*, *T. isabellina*, *T. malicola*, *T. variiformis*.

Red Pine (*Pinus resinosa*)

Secondary associates.—Pure (most abundant in Minnesota), or with jack pine, *Pinus banksiana;* white pine, *P. strobus;* pitch pine, *P. rigida;* also with hardwoods such as paper birch, *Betula papyrifera;* gray birch, *B. populifolia;* and aspen, *Populus tremuloides*, *P. grandidentata*.

Sites.—Sometimes dry, rolling, sandy land, but sandy loam, shallow rocky soils (often), and lake shores most favored; poorly drained areas seldom frequented. From Nova Scotia to northern Ontario and to southern Manitoba; in the east, south through parts of the northern states; also in Massachusetts, Pennsylvania, West Virginia, central Michigan, northern Wisconsin, and southeastern Minnesota.

Resupinate polypores.—*Fomes igniarius*, *F. igniarius nigricans*, *F. pini abietis*, *F. pinicola*, *Polyporus albolutescens*, *Pol. anceps*, *Pol. fragilis*, *Pol. pubescens*, *Poria byssina*, *P. candidissima*, *P. ferrea*, *P. laevigata*, *P. lenis*, *P. rixosa*, *P. rufa*, *P. subfuscoflavida*, *Trametes carbonaria*, *T. isabellina*, *T. odorata*, *T. variiformis*.

Yellow Poplar (*Liriodendron tulipifera*)
Yellow Poplar–White Oak (*Quercus alba*)

Secondary associates.—Beech, *Fagus grandifolia;* hemlock, *Tsuga canadensis;* basswood, *Tilia americana;* black birch, *Betula lenta;* cucumber, *Magnolia acuminata;* white ash, *Fraxinus americana;* buckeye, *Aesculus octandra;* black locust, *Robinia pseudoacacia*.

Sites.—Coves (particularly) and lower mountain slopes; ordinarily bottomlands on well-drained deep, moist soils, but soils sometimes relatively shallow and moist, occasionally nonfertile and acid. Particularly in Appalachian Mountains and in adjacent parts of the central forests, but also in sites from Vermont to Florida and west to Alabama, southern Illinois, Arkansas, and Mississippi.

Resupinate polypores.—*Fomes rimosus*, *Irpex cinnamomeus*, *Polyporus hirsutus*, *Pol. rutilans*, *Poria ambigua*, *P. andersonii*, *P.*

canescens, P. eupora, P. fatiscens, P. ferrea, P. laevigata, P. myceliosa, P. nigra, P. punctata, P. sericeomollis, P. spissa, P. unita pulchella, P. unita tenuis, P. versipora, P. viridiuscula, Trametes sepium.

Chestnut Oak (*Quercus montana*)

Secondary associates.—Red oak, *Quercus borealis maxima;* black oak, *Q. velutina;* post oak, *Q. stellata;* black jack oak, *Q. marilandica;* black gum, *Nyssa sylvatica;* black cherry, *Prunus serotina;* sourwood, *Oxydendrum arboreum;* silver bell, *Halesia carolina;* mountain laurel, *Kalmia latifolia.* In some areas, pitch pine, *Pinus rigida;* table mountain pine, *P. pungens;* shortleaf pine, *P. echinata.*

Sites.—Rocky upland soil, slopes, ridges, and sides of ravines with thin soils. From southern New England, New York (except Adirondack Mountains), Pennsylvania, New Jersey, and southward to Georgia and Alabama at elevations of from 1,500 to 4,000 feet.

Resupinate polypores.—Fomes pinicola, Irpex cinnamomeus, Polyporus gilvus, Pol. rutilans, Poria eupora, P. fatiscens, P. myceliosa, P. nigra, P. spissa, P. unita pulchella, P. unita tenuis, P. versipora, Trametes sepium.

Post Oak–Black Jack Oak (*Quercus stellata, Q. marilandica*)

Secondary associates.—Often black oak, *Quercus velutina;* white oak, *Q. alba;* scarlet oak, *Q. coccinea;* various hickories, mostly *Carya ovata, C. glabra,* and *C. cordiformis;* in some areas, shortleaf pine, *Pinus echinata;* loblolly pine, *P. taeda;* Virginia pine, *P. virginiana;* black gum, *Nyssa sylvatica;* southern red oak, *Q. rubra* L.

Sites.—Dry flats, uplands, or ridges mostly on heavy clay underlaid by hardpan or an impervious clay layer, with post oak predominating on heavy soils and black jack oak on light soils. Southern Massachusetts to northern Florida, but more particularly from Ohio westward into Oklahoma and eastward through southern part of central forest to southern Appalachians and Piedmont Plateau.

Resupinate polypores.—Fomes everhartii, Irpex cinnamomeus, Polyporus gilvus, Pol. hirsutus, Pol. rutilans, Poria fatiscens, P. myceliosa, P. unita pulchella, P. versipora, Trametes sepium.

Eastern Red Cedar (*Juniperus virginiana*)

Secondary associates.—Pure, or mixed chiefly with white ash, *Fraxinus americana;* shagbark hickory, *Carya ovata;* hackberry, *Celtis occidentalis;* in the northeast, with gray birch, *Betula populifolia;* red maple, *Acer rubrum;* in Arkansas, Mississippi, and eastward, with post oak, *Quercus stellata;* black jack oak, *Q. marilandica;* shortleaf pine, *Pinus echinata;* on limestone soils, with black locust, *Robinia pseudoacacia;* black oak, *Q. velutina;* white oak, *Q. alba.*

Sites.—Dry, gravelly, upland slopes or limestone outcroppings, sometimes wet land (but not deep swamps), rocky ridges, and abandoned pastures. Nova Scotia and New Brunswick west to Ontario, south to the coast of Georgia, the interior of southern Alabama, and Mississippi, and westward to eastern Texas; not ascending the Allegheny Mountains; in the Ozark uplift covering large areas of low, rolling, limestone hills.

Resupinate polypores.—Daedalea juniperina, Fomes annosus, Polyporus pinsitus, Pol. hirsutus, Pol. radiatus, Poria fatiscens, P. ferox, P. quercuum, P. unita pulchella, Trametes sepium.

River Birch–Sycamore (*Betula nigra, Platanus occidentalis*)

Secondary associates.—Red maple, *Acer rubrum;* black willow, *Salix nigra;* elm, *Ulmus americana.*

Sites.—Along rivers, at edges of creeks, and in swampy areas inundated for a part of the year. Southern New England, Maryland, Pennsylvania, southern Lake States (especially Wisconsin), tributaries of the Ohio, Mississippi, and Tennessee rivers, southern Appalachian Mountains, and Georgia westward to Oklahoma.

Resupinate polypores.—Fomes robustus, Lenzites trabea, Polyporus glomeratus, Pol. supinus, Pol. zonalis, Poria laevigata, P. undata, Trametes malicola.

Southern White Cedar (*Chamaecyparis thyoides*)

(Pl. V)*

Secondary associates.—Very often pure, but sometimes (usually as a result of fire) with red maple, *Acer rubrum;* black gum, *Nyssa sylvatica;* sweet bay, *Magnolia virginiana;* red bay, *Persea borbonia;* titi, *Cliftonia monophylla;* southern cypress, *Taxodium*

distichum; pond pine, *Pinus rigida serotina;* loblolly bay, *Gordonia lasianthus;* spruce pine, *P. glabra;* slash pine, *P. caribaea;* in the north, with gray birch, *Betula populifolia;* and, occasionally, pitch pine, *P. rigida.*

Sites.—Acid, peaty swamps underlaid by sand or clay, with water in the depressions for several months of the year. Coastal plain from southern Maine to northern Florida and southern Mississippi (Pearl River), but mostly in New Jersey, North and South Carolina, and western Florida.

Resupinate polypores.—*Polyporus caesius, Pol. dependens, Pol. dichrous, Pol. cinnabarinus sanguineus, Pol. ectypus, Pol. sector, Pol. supinus, Poria ferrea, Trametes subserpens.*

Southern Cypress–Hardwood (*Taxodium distichum; Nyssa aquatica* [Tupelo Gum], *Liquidambar styraciflua* [Red Gum])

Secondary associates.—Only rarely pure, cypress generally predominant, or with red maple, *Acer rubrum;* water oak, *Quercus nigra;* overcup oak, *Q. lyrata;* hackberry, *Celtis occidentalis;* American elm, *Ulmus americana;* water hickory, *Carya aquatica.*

Sites.—Sloughs, river bottoms, and bayou margins that are usually flooded for a long period. From southern Delaware and Maryland southward in coast region to southern Florida, westward to Texas, and, in overflow lands, throughout Mississippi and Louisiana, northward to southern Illinois.

Resupinate polypores.—*Fomes conchatus, Fomitiporia dryophila, Polyporus cinnabarinus sanguineus, Pol. dichrous, Pol. ectypus, Pol. gilvus licnoides, Pol. sector, Pol. supinus, Pol. zonalis, Poria ambigua, P. ferrea, P. flavomarginata, P. limitata, P. punctata, P. rufitincta, P. unita pulchella, Trametes carbonaria, T. odorata, T. subserpens.*

Pond Pine (*Pinus rigida serotina*)

Secondary associates.—Rarely, if ever, pure; in southern part of range, with slash pine, *Pinus caribaea;* farther north, with loblolly pine, *P. taeda;* pond cypress, *Taxodium ascendens;* red gum, *Liquidambar styraciflua;* sweet bay, *Magnolia virginiana;* swamp black gum, *Nyssa aquatica.*

Sites.—Flatwoods near the coast or near bays and ponds. Coastal

plain from southern New Jersey and North Carolina to Florida; Gulf coast of northern Florida.

Resupinate polypores.—Daedalea farinacea, Fomes annosus, Polyporus anceps, Pol. biformis, Pol. cinnabarinus sanguineus, Pol. dichrous, Pol. ectypus, Pol. pinsitus, Pol. semipileatus, Pol. supinus, Pol. zonalis, Poria albobrunnea, P. ambigua, P. canescens, P. cocos, P. ferrugineofusca, P. laevigata ludoviciana, P. lenis, P. luteofibrata, P. nigrescens, P. punctata, P. rufa, P. rufitincta, P. subfuscoflavida, P. undata, P. vaporaria, P. viridans, P. zonata, Trametes carbonaria, T. isabellina, T. odorata, T. subserpens.

Water Oak–Red Gum (*Quercus nigra, Liquidambar styraciflua*)

Secondary associates.—Willow oak, *Quercus phellos;* Nuttall's oak, *Q. nuttallii;* overcup oak, *Q. macrocarpa;* ash, *Fraxinus americana;* shagbark, *Carya ovata;* other hickories; black gum, *Nyssa sylvatica;* hackberry, *Celtis occidentalis;* cypress, *Taxodium distichum.*

Sites.—Low, wet bottom lands of coastal plain and land along large streams and deeper, narrow valleys in the upper Piedmont, especially where a shallow sheet of water covers the ground during the winter. New York to northeastern Florida, areas bordering the Gulf westward into Texas and low ground northward into Missouri, Kentucky, and Tennessee.

Resupinate polypores.—Fomes meliae, Fomitiporia dryophila, Irpex cinnamomeus, Polyporus caesius, Pol. cinnabarinus sanguineus, Pol. dichrous, Pol. ectypus, Pol. gilvus, Pol. gilvus licnoides, Pol. hirsutus, Pol. rutilans, Pol. supinus, Poria ambigua, P. ferrea, P. (Porothelium) fimbriata, Poria flavomarginata, P. nigrescens, P. punctata, P. spiculosa, P. unita pulchella, P. vulgaris, P. versipora, Trametes sepium, T. subserpens.

Live Oak–Cabbage Palmetto (*Quercus virginiana, Sabal palmetto*)
Cabbage Palmetto

Secondary associates.—A large number of genera and species, often including *Eugenia spp.;* sweet bay, *Magnolia virginiana;* wild fig, *Ficus aurea;* fig, *F. brevifolia;* red gum, *Liquidambar styraciflua;*

wild tamarind, *Lysiloma bahamensis;* and loblolly pine, *Pinus taeda.*

Sites.—Dry or relatively moist, sandy, bay shores, beach dunes, salt-water estuaries, and calcareous hummocks. North Carolina southward along the coast and islands in rich hummocks to southern Florida; along the coast of the Gulf of Mexico through east Texas on ridges a few feet above the level of the sea.

Resupinate polypores.—*Fomes conchatus, Fomitiporia dryophila, Polyporus cinnabarinus sanguineus, Pol. corrosus, Pol. dichrous, Pol. gilvus licnoides, Pol. hydnoides, Pol. sector, Pol. trichomallus, Poria borbonica, P. bracei, P. fatiscens, P. heteromorpha, P. limitata, P. mollusca, P. punctata, P. subfuscoflavida, P. unita pulchella, P. versipora, Trametes carbonaria, T. subserpens.*

Specific Description

Poria vaillantii (Fries) Cooke, Grevillea, 14: 111. 1886

(Pl. VI)

Boletus vaillantii De Candolle, Flore française, 6: 58. 1815.
Physisporus vaillantii (DC) Gillet, *in* Karsten, Hattsv., 2: 63; Finl. Bas., 322. 1889.
Polyporus vaillantii (DC) Fries, Syst. Myc., 1: 383. 1821.

Important specimens examined:

Poria vaillantii DC on Abies grandis, Clarksia, Idaho. Det. Bresadola. Herb. Kew, London, England.
Poria vaillantii Fries. Det. Bresadola. Herb. Kew, London, England.

Fructification annual, effused in patches, often extending out as white fans of mycelium and rhizomorphic cords for 2 or more centimeters, easily separating, soft but not very fragile, membranaceous; margin white, broadly sterile sometimes for 4 cm. or more; subiculum white, soft, coriaceous; tubes mostly less than 1 mm. long, occasionally 2–2.5 mm.; mouths white or whitish when fresh and usually remaining so, sometimes becoming slightly "cinnamon buff" (Ridgway), subcircular to subangular, thin-walled, entire or dentate, 2–3 to a mm.; basidia 6–8 × 15–25 μ; spores ellipsoid or oblong-ellipsoid, smooth, hyaline, 3–4 × (5) 5.5–7 μ; hyphae seldom branched; clamp connections present, 2–4 μ in diameter; no cystidia.

Allied species.—*Poria vaillantii* should be compared with *P. sinuosa,*

since many specimens of *P. sinuosa* in herbaria have been identified as *P. vaillantii*. *P. sinuosa*, according to Swedish collections, is interpreted in Sweden and in this paper as a growth form of *P. vaporaria*. Romell (7) believed that *P. sinuosa* and *P. vaporaria* as interpreted at first by himself and by Bresadola are, in all probability, identical plants. The cylindrical or allantoid spores of this form of *P. vaporaria*, in which the mouths have become somewhat dentate, may be used to distinguish it from *P. vaillantii*.

There has always been some uncertainty about plants named "mollusca," chiefly due to confusion in the nomenclature rather than to difficulties in distinguishing the plants. Many collections have been called "mollusca" of Fries or of Persoon. These have been variously interpreted as *Poria vaillantii*, *P. vaporaria*, and *P. mucida*. The name "mollusca" is used here for the soft, white, or sometimes almost cream-white, plant which Bresadola interprets to be *P. mollusca* of Persoon. This designation was followed by Romell. The fungus is the *P. mollusca* of contemporary Swedish scholars. Because of the softness of *P. vaillantii*, the plant might be confused with *P. mollusca*, but the spores of *P. mollusca* are 2.5–3 (4) × 2–2.5 μ and so are much smaller than those of *P. vaillantii*, which are 3–4 × (5) 5.5–7 μ.

Habitat.—*Abies grandis*, *Carya glabra*, *Castanea spp.*, *Citrus limonia*, *Lyonothamnus spp.*, *Pinus ponderosa*, *P. rigida* (8), *P. strobus* (8), *Pseudotsuga taxifolia*, *Sequoia sempervirens*, *Taxodium distichum*, *Thuja plicata*, *Tsuga canadensis* (8), *T. heterophylla*.

It has been found on flower pots, linoleum, tree-fern moss, and in damp environments such as basement timbers might afford. Notes accompanying specimens in various herbaria read "on pine boards in cellars," "found in a cellar," "botanical-garden benches," "underground near plants," "on flower pots buried in a heavy soil," and "on mine props."

Distribution.—Alaska; Manitoba, Ontario, Quebec (6); California, Connecticut, Idaho, Maryland, Massachusetts, Michigan, Nebraska, New Jersey, New York, North Carolina, Oregon, Pennsylvania, Virginia.

Occurrence.—The fungus is seemingly more widely distributed in northern and central Europe and in England than in North America. Because it can grow at a greater range of tempera-

tures than *Merulius lacrymans*, it is found in many English mines in which the temperature is too high for Merulius (4). *Poria vaillantii* is common on greenhouse benches, but apparently its place as an important cause of decay in structural timbers on the American continent is taken by *Poria incrassata*, *Polyporus* (*Trametes*) *serialis*, or *Poria xantha*.

Cultures.—Hyphae are wider than those of most wood-destroying fungi, according to Cartwright and Findlay (4), for they average 5–6 μ, and, occasionally, inflated hyphae in the submerged mycelium are up to 18 μ in diameter. Large clamp connections appear. A few chlamydospores develop in the submerged mycelium.

Growth features have been described by Cartwright and Findlay (4). The fungus grows fairly rapidly on malt agar, exhibiting at the optimum temperature of 27° C. a daily increment in diameter of 12.5 mm. The maximum temperature for growth is approximately 36° C., and therefore, as has been said, the fungus is tolerant of a much wider range of temperature than in *Merulius lacrymans*. *Poria vaillantii*, however, requires more moist conditions for its development than does *M. lacrymans*. *P. vaillantii* gives a negative reaction to tannic-acid medium (5), and is fairly resistant to antiseptics, especially those in which the toxic element is copper (4).

Decay.—Gross features: *Poria vaillantii* produces a carbonizing rot in structural timbers. The mycelial cords remain pliable and do not become hard and brittle as do the rhizomorphs of many fungi.

The whitish, ropy rhizomorphs of *Poria vaillantii* may be distinguished usually from mycelial mats of *P. incrassata* by their color and consistency. Fruiting bodies of *P. vaillantii* are never blackish, orange, or decidedly yellow, as they often are in *P. incrassata*, and the spores of *P. vaillantii* are not colored, but hyaline. Ends of beams which rest in damp brick walls are subject to attack by the fungus. Similarly, areas between the subflooring and the top flooring and timbers about porches furnish favorable environments for it. *P. vaillantii*, however, is not so common as *P. incrassata* in America and not nearly so important.

Microscopic features: These have been described by Cartwright and Findlay (4). Hyphae in decayed wood are moder-

ately numerous. Most of them measure 2–5 μ in diameter, but some are as much as 8 μ. Clamp connections are not numerous. Oval, pear-shaped chlamydospores measure up to 3 $\times$ 8–10 μ, especially in the tracheids. Hyphae make cylindrical holes which average 3 μ in diameter.

Importance.—*Poria vaillantii* is not important in North America except locally, where it has appeared on greenhouse benches.

In England, Cartwright and Findlay (4) report that the fungus is probably the most important agent of decay in damp mines. It rots "pitprops in damp return air-ways with amazing rapidity, often rendering them useless in less than a year." According to these authors, it is described by Pilat as one of the most dangerous fungi in mines, producing great masses of superficial growth which run over the coal face and infect props. It is said to be the most common species of Poria on railroad ties (sleepers) in Poland, and it is this species (not *P. vaporaria*) that is common in houses there. *P. vaillantii* is reported to be a common cause of dry rot in buildings where leakage has occurred, but it does not spread to the drier parts of a building as *Merulius lacrymans* sometimes does. The mycelial strands do not penetrate deeply into brickwork, and eradication is, therefore, simpler than with *M. lacrymans*.

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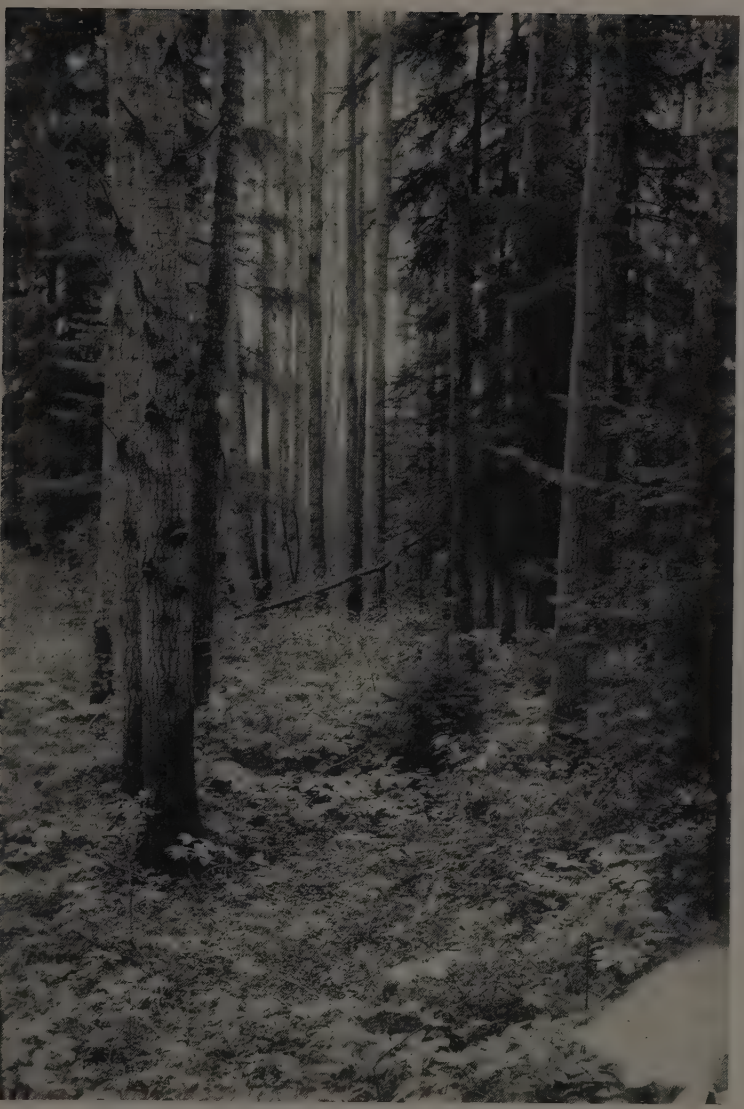
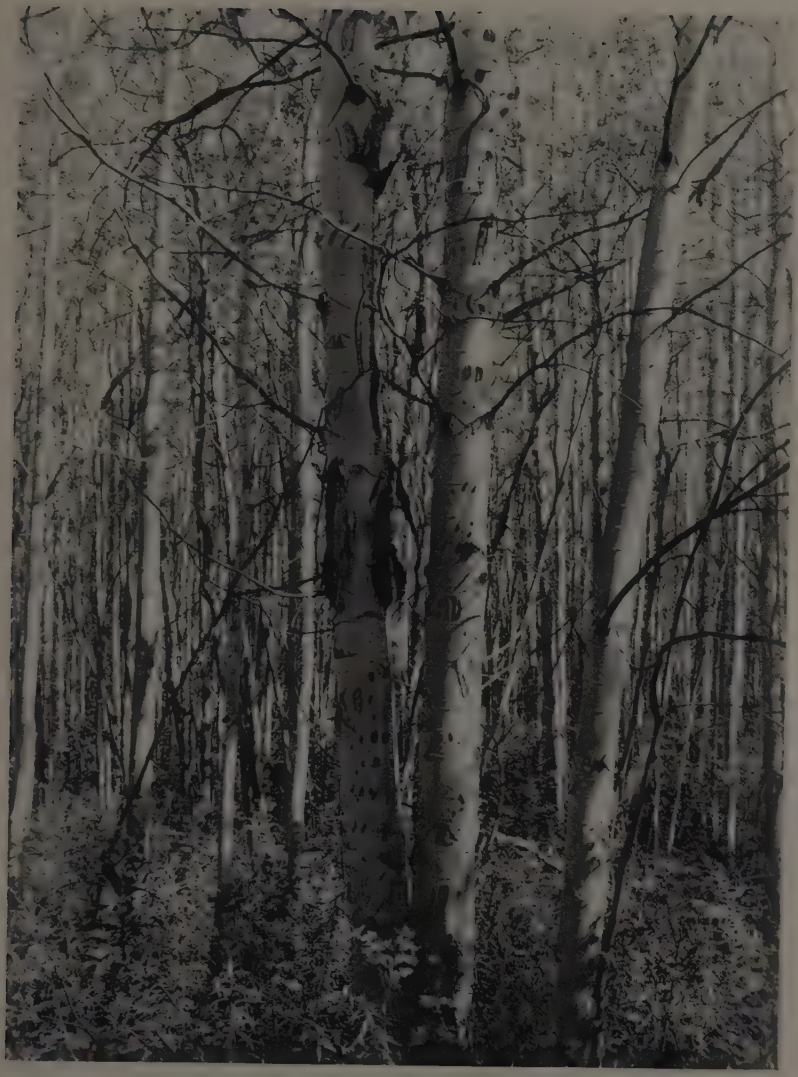
Cottonwood forest along the Red River, Grand Forks, North Dakota



Stand of *Populus grandidentata* severely infected with *Fomes igniarius;* forest on basaltum, Athabasca River, Alberta, Canada



Populus tremuloides in the Cassiar district of northern British Columbia

Pinus banksiana association, Fort Wrigley, Northwest Territories

Chamaecyparis thyoides, Lebanon State Forest, New Jersey

Poria vaillantii (Fries) Cooke on coniferous boards in a greenhouse in Moscow, Idaho